The Energy Cost of Walking and Cycling in Young and Older Adults

by

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ABSTRACT

The effects of aging on muscular efficiency are controversial. Proponents for increased efficiency suggest that age-related changes in muscle enhance efficiency in senescence. Exercise study results are mixed due to varying modalities, ages, and efficiency calculations. The present study attempted to address oxygen uptake, caloric expenditure, walking economy, and gross/net cycling efficiency in young (18-59 years old) and older (60-81 years old) adults (N=444). Walking was performed at three miles per hour by 86 young (mean = 29.60, standard deviation (SD) = 10.50 years old) and 121 older adults (mean = 66.80, SD = 4.50 years old). Cycling at 50 watts (60-70 revolutions per minute) was performed by 116 young (mean= 29.00, SD= 10.00 years old) and 121 older adults (m = 67.10 SD = 4.50 years old). Steady-state sub-maximal gross/net oxygen uptake and caloric expenditures from each activity and rest were analyzed. Net walking economy was represented by net caloric expenditure (kilocalories/kilogram/min). Cycling measures included percent gross/net cycling efficiency (kilo-calorie derived). Linear regressions were used to assess each measure as a function of age. Differences in age group means were assessed using independent t-tests for each modality (alpha = 0.05). No significant differences in mean oxygen uptake nor walking economy were found between young and older walkers ($p>0.05$). Older adults performing cycle ergometry demonstrated lower gross/net oxygen uptakes and lower gross caloric expenditures ($p< 0.05$).

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TABLE OF CONTENTS

Page

APPENDIX Page

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER 1

INTRODUCTION

DEFINITIONS

Work. Energy expended; expressed in kilocalories or represented by the volume of oxygen uptake.

Work rate. energy expended at a given speed; expressed in watts per minute at a given cadence (cycling) or miles per hour (walking).

Speed. Velocity as expressed in revolutions per minute (cycling) or meters per minute (walking).

Indirect calorimetry. measurements of oxygen uptake and carbon dioxide eliminated in a given time period while performing a given activity. May be used to calculate work as expressed by caloric expenditure.

Muscular efficiency. Encompasses metabolic and contractile muscular efficiencies; the product of phosphorylative and mechanical coupling efficiencies.

Phosphorylative coupling efficiency. The mitochondrial capacity to generate ATP via aerobic metabolism (i.e. the degree of pairing between the electron transport system and activity of ATP synthase). Also referred to as mitochondrial coupling efficiency herein. In other text also referred to as chemo-mechanical or chemiosmotic coupling. Expressed by the P/O ratio.

Contractile coupling efficiency: The muscle fiber's capacity to utilize ATP generated to perform mechanical work

Gross (mechanical) efficiency for cycling: The amount of work accomplished (caloric equivalent) for the total energy expended (kilocalories) while performing that work; includes resting energy expenditure:

$$\text{Gross efficiency} = 0.717 \,/\, \text{Cycling caloric expenditure} \quad (1)$$

Where 0.717 is the caloric equivalent of 50 watts

Net (mechanical) efficiency for cycling: The amount of work accomplished for energy expended above that (which is) expended at rest; does not include resting energy expenditure:

$$\text{Net efficiency} = 0.717 \,/\, \text{Cycling caloric expenditure} - \text{resting caloric expenditure} \quad (2)$$

Gross walking economy: The gross cost of walking at a given speed as represented by caloric expenditure (kcal/kg/min).

Net walking economy: Net Caloric expenditure (above those at rest) for walking at a given speed (kcal/kg/min):

Net walking economy = walking caloric expenditure - resting caloric expenditure (3)

Young participants: For the purpose of this study, those 18-59 years old were classified as young participants. This is relative to the ages of older participants.

Older participants: For the purpose of this study, those 60-81 years old were classified as "older participants." This is relative to the ages of "young participants".

DELIMITATIONS AND LIMITATIONS

Limitations to the study include the use of a single work rate, the use of gross and net efficiency calculations (as opposed to delta efficiency), and an unequal distribution of subject characteristics between modalities such as: disparities in the numbers of younger and older individuals; only one subject exceeding eighty years of age, and uneven gender distributions. In addition, middle-aged adults were not included in the study, and physical activity and peak work rates between the young and the old performing each modality were not assessed. Delimitations include a large sample number and age groups displaying a wide spread of age ranges in both young (18-59) and older (60-81) subjects groups. The study also utilized dual modalities (cycle ergometry at 50 watts, 60-70 rpm and submaximal level treadmill walking at 3 mph) to perform steady-state submaximal work.

CHAPTER 2

REVIEW OF LITERATURE

In 2013 a debate appeared in the Journal of Applied Physiology: Venturelli and Richardson stated that "healthy aging is associated with increased mechanical efficiency" while Ortega insisted that muscular efficiency decreases with age (Venturelli & Richardson, 2013; Ortega, 2013). The former authors posit that since aging is associated with a loss of type II fibers muscular efficiency increases. The latter proposes that age-related mitochondrial dysfunction results in decreased efficiency.

The basis of Venturelli & Richardson's argument is that sarcopenia preferentially affects type II fibers in older individuals which results in an increase in muscle metabolic efficiency. The increase in muscle metabolic efficiency is reflected in improvements in mechanical efficiency with senescence. Ortega believes that observed reductions in mechanical efficiency are due to compromised mitochondrial efficiency with age.

In the debate, each of the authors first cites various supportive studies which examine muscle at the tissue and cellular levels. These include studies on fiber type composition, contractile velocity, myofilament changes, neural activation, muscular fatigue, and mitochondrial alterations. The authors further cite studies which compare the energetic costs of physical activity (the associated efficiencies and economies) between younger and older participants. However, the overall body of literature on this subject remains inconclusive.

This is due in part to study differences in subject attributes, activity modalities, measurement protocols, and calculations. The validity of some studies as supportive evidence has also been questioned due to the use of one-minute exercise data. Thus, the following review aims to discuss these issues and their relevance to future studies. It addresses the points made by each protagonist, beginning with mechanistic propositions. The cited activity studies are subsequently examined and the differences between them are addressed. Finally, some gaps in the existing physical activity literature are identified.

BACKGROUND PHYSIOLOGY

Muscular efficiency. "Muscular Efficiency" describes a.) The muscle fiber's capacity to utilize the Adenosine triphosphate (ATP) generated to perform mechanical work (i.e. contractile coupling) and b.) The mitochondrial capacity to generate ATP (phosphorylative coupling). Each is important to the discussion of age and efficiency; age-related cellular morphological and functional changes have been observed in both coupling processes (Hiona and Leeuwenburgh, 2008; Thompson, 2009; Conley, Amara, Jubrias & Marcinek, 2006; Cartee, 1994).

Fiber contraction. Prior to contraction, the myosin head is literally wrapped around ATP. Tension at the myosin crossbridge exists because the myosin head is "pulled back" during a state of myosin-actin coupling inhibition.

The inhibition is caused by the binding of troponin and tropomyosin on the actin filament. When Ca^2+ binds to a receptor on troponin, troponin-tropomyosin is no longer able to bind to actin. Myosin binds with actin, which stimulates ATPase to hydrolyze ATP. Energy from the hydrolysis of an ATP releases the "cock" of the cross bridge (it straightens because the myosin head is no longer pulled back). The release of potential energy stored as tension thus causes the actin and myosin filaments to slide over one another.

The process of phosphorylative coupling. Phosphorylative coupling occurs inside of the mitochondria and has two main segments: 1.) the electron transport system (ETS) and 2.) ATP synthesis. At the starting point of the ETS, the nicotinamide adenine dinucleotide (NADH) and flavin adenine dinucleotide ($FADH_2$) resulting from glycolysis, beta oxidation, and the Krebs Cycle are reduced to NAD and FAD. The hydrogen anions (or dissociated electron pairs) travel through their respective complexes of the ET chain within the inner mitochondrial membrane. NADH electrons pass through complexes I, II, and IV before returning to the matrix where oxygen finally receives the electrons. Similarly, two electrons from $FADH_2$ pass through complexes II-IV. The presence of the electrons passing through the complexes causes the complexes to pump hydrogen protons into the intermembrane space (complexes I and III release four protons; and complex IV releases two). Thus, a proton gradient is formed wherein the intermembrane space has a higher positive H+ charge relative to the lower H+ charge of the matrix.

In order for the protons to flow from the higher charge of the intermembrane space to the lower charge of the matrix, they must pass through ATP synthase. ATP synthase is the "lollipop"-shaped structure embedded in the inner mitochondrial membrane which is responsible for ATP generation. The FI "head" appears as a knob that sits on the membrane and resides in the matrix, while the adjoining FO portion (i.e. the "stick") penetrates the membrane. Protons use the FO portion of ATP synthase as a "channel" from the intermembrane space to the FI head.

Rather than simply passing protons through FI to the matrix, the structure "harvests" the potential energy of the ETS and uses the protons to form ATP. It does so via three binding site pairs: one is empty (the "O" site), one contains ADP (adenosine diphosphate; the "L" site), and another contains ATP ("T" site).

These three configuration types are able to alter their configurations concomitantly so that each type is always present. Thus, when a proton enters the L site and binds to ADP, the T site relinquishes its ATP into the matrix and becomes an “O” site. As each binding site alters its formation, the structure rotates. Therefore, rotation is “coupled” to the FI reactions of ATP synthesis.

Similarly, the action of the ETS is coupled to the phosphorylation of ADP to ATP in the process of phosphorylation. Hindering one process invariably impairs the other and an “uncoupled” system becomes ineffective. Thus, the term “mitochondrial efficiency” describes the extent to which the action of the ETS is coupled to the phosphorylation of ADP to ATP. It is expressed as the P/O ratio, or the number of ATP generated for each electron pair donated. (“P” refers to the phosphates bound during ATP synthesis and “O” to the substrate oxidation which provides the electron pairs for transport). P/O ratios differ among skeletal muscle; but a suggested standard for optimal coupling is 2.5; mild uncoupling for human lastus vasteralis muscle is 2.0 (Conley et al., 2006).

PROPOSED MECHANISMS FOR DECREASED EFFICIENCY

Aging and oxidative phosphorylation. Age-related mitochondrial changes may be problematic when they significantly interfere with coupling processes. In the 2013 Point: Counterpoint debate between Ortega and Venturelli & Richardson, Ortega cites Harper, Bevilacqua, Hagopian, Weindruch, & Ramsey in stating that leakage of the H+ hydrogen pump is implicated in decreased coupling efficiency (2004).

Uncoupling is believed to be a protective measure from potential oxidative damage initiated by reactive oxygen species (ROS). Mitochondrial ROS formation occurs at various sites and quantities, especially during aerobic metabolism. The largest sites of ROS formation occur at complexes I and II of the ETS (Sizbor & Holtz, 2003). However, uncoupling proteins (UPCs) are able to mitigate ROS generation by way of H+ leakage. As protons leak into the matrix, the inner mitochondrial membrane is depolarized and the protonmotor forces used to power ATP synthesis decrease (Harper et al., 2004). ROS production subsides. Thus, ROS production is subdued at the expense of ATP synthesis.

Not surprisingly, the proton-motive forces observed in the skeletal muscle of young rats are higher than those observed in old rats across varying levels of oxygen consumption (Harper et al. 2004). The observation supports and unifies the "Rate of Living" and "Free Radical" hypotheses of aging described above (Sizbor & Holtz, 2003): Older mitochondria may operate at decreased (coupling) efficiency in order to prolong life by preventing further accumulation of oxidative damage. In Ortega's view, decreased phosphorylative coupling efficiency results in an overall decrease in muscular efficiency. He proposes that the favorable alterations cited by Venturelli & Richardson (discussed below) are insufficient to outweigh the deleterious effects of aging.

PROPOSED MECHANISMS FOR INCREASED EFFICIENCY

Meanwhile, Venturelli & Richardson (2013) propose that the changes cited by Ortega ultimately increase efficiency. They cite limitations to exercise studies supporting decreased mechanical efficiency while offering mechanistic and activity studies in support of increased efficiency (2013). Their theory is that sarcopenia in senescence ultimately increases mechanical efficiency (defined as the ratio of work accomplished to oxygen consumed).

Venturelli & Richardson's argument is as follows:

Sarcopenia increases metabolic efficiency. A greater number of type I fibers relative to the number of type II fibers might be viewed as advantageous when considering energy utilization and production. This is because different fiber types predominantly rely on different means of energy production (McArdle, Katch and Katch, 2006) and have different rates of energy utilization. Type IIb fibers have a high relative force production and a faster contractile velocity than the other fiber types. A faster contraction rate means that type II fibers utilize more ATP relative to type I fibers per given amount of time, which makes them more metabolically costly.

In addition to requiring more ATP, type II fibers contain less mitochondria and fewer oxidative enzymes . This means that type II fibers produce little ATP. The smaller ATP production is due to faster contractile velocities. Fast contractile velocities require the use of faster systems of ATP production (Phosphocreatine, PCr, and anaerobic glycolysis).

These systems are not delayed by the time taken for oxygen to diffuse across the pulmonary membrane, enter the heart, and finally reach muscle because they do not require the presence of oxygen. However, these systems are inefficient in ATP generation. PCr uses one phosphate to form one ATP. Anaerobic glycolysis forms two ATP per molecule of glucose, and three ATP per molecule of glycogen. Thus PCr and anaerobic glycolysis have production ratios of 1:1 or 1:2 and 1:3, respectively (Dunford & Doyle, 2012).

Conversely, Type I "slow-twitch" fibers have slow contraction speeds which allows them to rely primarily on aerobic energy production (oxygen molecules are the final recipients of NADH and FADH2 electrons dissociated in the ETS). Aerobic ATP production may take longer but it is vastly more efficient than either PCr or anaerobic glycolysis: the complete oxidation of a single molecule of glucose yields an estimated 32-36 ATP (Dunford & Doyle, 2012).

In addition to the superior ATP generation capacity of aerobic metabolism, the researchers state that the cost of sustaining the slower "twitch rate" of type I muscles is less than that required to sustain the "fast-twitch" of type II fibers. Thus, overall efficiency may increase with an increase in type I fibers.

Slower contractile velocity of type I fibers. The unloaded sliding velocity of isolated type I filaments themselves also appears to decrease: isolated type I muscle from the vastus lateralis muscles older mice, rats, and humans were 18-25% slower than those of younger subjects (Hook, Sriramoju, & Larsson, 2001). Age-related changes to the myosin molecule and related enzymes including ATPase may be responsible. Venturelli & Richardson's second statement is that age-related decrements in the contractile velocity of type I muscles may further reduce the metabolic cost of type I contraction which is already comparatively low.

Slower contractile properties. Slower contraction rates would thus reduce the overall necessity of ATP and diminish the need of Ca2+ release from the sarcolemma. Less Ca^2+ released means that there is less Ca^2+ to unbind and the cost of breaking the actin-myosin bond (to return Ca^2+ to troponin) would also be reduced. Thus the colleagues suggest that the metabolic cost of type I contraction decreases.

Altered force-frequency relationship. Thirdly, slower contractile velocity is accompanied by slower relaxation, which delays the return of force to baseline levels (Allman & Rice, 2004). When the relative relationship between force outputs and low vs. high frequency stimulation is graphed, there is a "leftward shift" in older adults as compared to younger ones. In other words, higher intermittent stimulation frequencies are needed to generate maximal force in older adults during intermittent stimulation. This implies a negated necessity to recruit type II fibers which deliver greater power but have a higher metabolic cost. Therefore, Venturelli & Richardson (2013) suggest that "age-related changes in skeletal muscle phenotype (i.e. a greater percentage of type I fibers) may work synergistically with changes in activation pattern" to increase metabolic efficiency in senescence.

A decreased cost of maintaining the calcium pump. Finally, Venturelli & Richardson (2013) site this "leftward shift" as support for increased muscular efficiency. They state that "the higher relative force at lower stimulation frequencies in older skeletal muscle likely reduces the energy required for ion transport and lessens the motor drive needed to maintain a given workload".

As previously mentioned, muscular contraction is initiated when Ca^2+ binds to the troponin- tropomyosin structure thereby allowing myosin to couple with actin (McArdle et al., 2006). This is evident in the fact that neural stimulation of type II fibers results in an increase in Ca^2+ concentration which is three times as high the concentration increase occurring with type I stimulation (McArdle, et al., 2006). A lesser concentration of Ca^2+ is advantageous because when neural stimulation ceases Ca^2+ must be actively pumped back into the lateral vessels of the sarcoplasmic reticulum, which requires energy. The cost of the calcium pump in type II muscle is an estimated 5-10 times higher than that of type I muscle (Wendt and Gibbs, 1973, as cited by Venturelli & Richardson, 2013). Therefore, a reduction in type I contractile velocity would further reduce the relative cost of ion handling at the cellular level.

EXERCISE STUDY CONSIDERATIONS

Both protagonists offer compelling arguments for their hypothesis. Nonetheless, exercise study results remain equivocal (Review of previous study results in Appendices A and C). After considering the speed/ efficiency relationship and the assumptions of estimating muscle metabolism, comparative studies cited by each proponent are reviewed below.

The efficiency-speed relationship. In general, the linear relationship between work rate and oxygen uptake (VO_2) dictates a constant muscular efficiency across a wide range of power outputs. Because VO_2 increases with pedaling speed at a constant power output, cycling efficiency tends to decrease as pedaling cadence increases (Gaesser and Brooks, 1975). Similarly, when pedaling at a constant cadence, cycling efficiency decreases with increases in power output because VO_2 rises with increasing force production at a constant pedaling cadence.

The VO_2-speed relationship in walking is "U" shaped (Larish, Martin, & Mungiole,1988). This suggests that there is a speed range at which walking economy is highest (the authors suggest a range between 1.1 and 1.3 m/sec). Walking at speeds above and below this range tends to yield higher metabolic costs. In other words, the oxygen uptake during walking increases with speed at a constant grade, but walking at very low speeds also decreases economy by increasing oxygen uptake. When walking at a constant speed, VO_2 increases with increases in incline and decreases with decreased incline (Hortobagyi, Finch, Solnik, Rider, & DeVita, 2011).

Approximating oxygen consumption of muscle. In 1992 Poole, Gaesser, Hogan, Knight & Wagner demonstrated a tight linear relationship between both pulmonary and leg VO_2 with work rate ($r = 0.999$ and 0.989, respectively). Moreover, the investigators established that the slopes of the pulmonary vs. leg consumption values were nearly identical across the same cycling work rates (0.0099 vs. 0.0092, respectively, $p < 0.05$). Consequently, pulmonary oxygen consumption measured at the mouth is representative of oxygen consumption in the working muscle.

The investigators note a disassociation of the relationship for smaller muscle groups since a smaller portion of muscle mass allows more room for VO_2 increase at sites outside of the muscle. The assumption that pulmonary VO_2 accurately reflects leg VO_2 is also dependent upon the subject exercising at a submaximal "steady state".

Here, mitochondria can maintain a balance between ATP generation and ATP utilization. The presence of the metabolic byproduct lactate is minimal and easily recycled. However, as exercise intensity increases, the rate of ATP turnover does as well and the body increasingly relies on anaerobic sources of energy production. As a result, lactate begins to accumulate in the blood.

Since the association of oxygen to heme is pH sensitive, accumulated lactate must be buffered. The body is able to use carbon dioxide to do so. A respiratory exchange ratio (RER) which exceeds 1.0 signifies that a greater amount of carbon dioxide is being blown off than the amount of oxygen consumed, and ATP production is primarily anaerobic.

It generally takes at least two to three minutes for an individual to "reach steady state" at the onset of exercise or for a given change in submaximal intensity level. Therefore, the use of pulmonary VO_2 to approximate muscular VO_2 is not valid if values are derived from non-steady state activity, or intense exercise which exceeds muscle's aerobic capacity (RER >1.0).

Ortega (2013) states that for this reason studies which derive oxygen consumption rates obtained during a single minute for each power level evaluated are questionable. He also notes that the technique likely underestimates metabolic energy consumption while overestimating efficiency, and that this effect may be magnified for older adults due to slower oxygen uptake kinetics. Therefore, preserving the pulmonary to muscle VO_2 relationship is key when developing graded exercise protocol or collecting representative VO_2 values for studies which aim to examine metabolic muscular efficiency.

STUDIES IN SUPPORT OF DECREASED EFFICIENCY

Walking. Some walking studies (Mian, Thom, Ardigo, Narci, & Minetti, 2006; Hortobagyi et al., 2011; Woo, Derleth, Stratton & Levy, 2006 ; Ortega & Farley, 2007; Larish, et al., 1988; Malatesta et al., 2003) have suggested that muscular efficiency decreases with age (Appendix A). Efficiency determinations between these studies varied slightly (Appendix B). Some studies simply used the increased gross oxygen consumption in the elderly to infer a decrease in metabolic efficiency relative to the young when walking at equal speeds (Hortobagyi et al. 2011; Larish et al., 1988; Malatesta et al., 2003 ; Ortega & Farley, 2007). Others made the same deduction in citing differences in net walking metabolism and calculated walking efficiencies (Mian et al., 2006, & Woo et al. 2006).

Hortobagyi et al. Hortobagyi and colleagues published a study addressing the association between agonist/antagonist muscle co-activation and the cost of walking (Appendix A). Subjects were 12 healthy young (m = 6, f = 6 ; 20 ± 2.2 years old) and 12 healthy older adults (m= 5, f =7 ; 77.4 ± 4.8 years old). Exercise protocol included six minutes of level treadmill walking at 0.98 m/sec. Energy expenditure for six minutes of stationary standing was also collected ; all values were two-minute steady state averages (RER <1). Gross and net VO_2 were used to calculate net metabolic rate, and the cost of walking was expressed as net metabolic rate/speed (J/kg/m).

The cost of level walking was 2.61 ± 0.14 J/kg/min; p=0.16 in older adults and 3.09 ± 0.12 J/kg/m in younger adults walking at the same speed (0.98 m/sec, p = 0.013). When values were normalized for mass and distance the cost of walking was 19% higher for older adults than for the young (p = 0.013) .

Unique study aspects were the inclusion treadmill grade variations (-6%, level, +6%), a close pairing between subjects (height, mass, BMI, standing VO_2, preferred walking speed, Short Physical Performance Battery test scores), and group differences in co-activation levels at each grade. Energy cost increased with grade and decreased with decline for both groups (p = 0.01).

However, older adults had greater antagonist co-activation, oxygen uptake, and a higher cost of walking than the young during decline and level protocols ($p < 0.05$). Only results for the level protocol (normalized for distance and speed) are shown in Appendix A.

***Ortega & Farley*.** Ortega also cites himself & Farley (2007) for their investigation on mechanical limb work and the higher metabolic cost of walking in older vs. younger adults (Appendix A). The investigators compared the VO_2's of 10 healthy older adults (76 ± 4 years) and 10 young adults (25 ± 4 years) at five different treadmill walking speeds (0.7, 1.0, 1.3, 1.5, and 1.8 m/sec; grade 0%). The values are the average steady-state VO_2's obtained between minutes four and seven, when RER values were <1.0.

Results indicated that older subjects consumed about 20% more oxygen than younger subjects for one meter of travel across speeds (J/kg/m/sec; $p = 0.010$). When walking at 1.0 m/sec (the speed deemed most economical for both groups), older individuals had a 17% greater cost of transport than the young. Difference in net metabolism (VO_2) between groups increased with speed, and older individuals had higher consumption rates than the younger adults at the slowest (14% greater) and fastest speeds (34% greater) ($p = 0.01$) (oxygen consumption not included in Table 1).

Woo et al. Meanwhile Woo et al. (2006) are cited for reporting lower walking efficiencies in older adults as compared to the young during an exercise intervention study (Appendix A). Subjects were healthy younger women (n= 15; ages 20-33), younger men (n=12; ages 20-30), older women (n=16 ; ages 65-79), and older men (n=18; ages 65-77).

The results most relevant to this discussion come from two minutes of treadmill walking at 3.5 miles per hour after two minutes of seated rest (Appendix A). Here, net oxygen consumption was higher in the older subjects as compared to the young (9.9 ± 1.3 vs. 11.8 ± 2.4 ml/kg/min ; 1.9% net VO_2 difference; $p<0.0001$). Younger participants also had greater walking efficiencies for this condition (20.9 ± 3.0 vs. 17.3 ± 3.1% = 3.6% greater net metabolic cost $p<0.0001$). Post-training values show a greater improvement in peak VO_2 for older adults (16%) as compared to the young (7%) ($p=0.03$); and a similar trend in efficiency values (older adults = 21%, younger adults = 6%; $p = 0.09$).

Other study contributions include results from the other five treadmill protocols. However, these do not provide an absolute means of comparison because not all protocols were performed by every subject. Assignment was based off of estimated fitness levels. Though they do not detail the protocols (grade changes or minutes per stage), the authors state that maximal speeds were 3.5, 4, 4.5, 5, and 6 miles per hour and that "most subjects achieved a peak RER of 1.0". Since consistent steady state RER values (>1.0) cannot be confirmed, VO_2 and efficiency measures are not reflective of muscular efficiency. Nonetheless, the findings may be of interst : younger participants had mechanical efficiencies of 22.2 ± 2.4 % and older participants were about 8% less efficient with efficiencies of 20.4 ± 3.7% (p=0.03). (Post-training data show that the young did not significantly improve efficiency (2%; p = 0.42) while exercise efficiency for older individuals increased by 31%, p<0.0001).

Mian et al. A significant study by Mian et al. (2006) examined walking efficiency and gross and net energy costs of level treadmill walking at various speeds (Appendix A). Subjects consisted of 12 healhty young (27± 3 years) and 20 healthy older (74 ± 3 years) men. Relevant study results include the follwing findings:

1.) The net energy cost of walking (joules) was an average of 31% higher in old vs. young subjects across speeds (.83, 1.11, 1.39, and 1.67 m/sec ; F_{age}= 12.8 ; p< 0.01 ; Table1).
2.) In older subjects percent efficiency decreased with speed to a greater extent than it did in younger subjects (F_{age} x speed = 4.2, P<0.05).
3.) Results support a decrease in walking efficiency in older subjects.

Other noteworthy study aspects are subject matching for leg lengths and masses in order to differentiate between internal and external work, and to examine antagonist muscle co-activation between groups.

Malatesta et al. (2003) conducted an investigation which is notable for its inclusion of two groups of older subjects (Appendix A). The investigators had ten 80 year olds, ten 65 year olds, and ten 25 year olds participate in treadmill walking at 0.67, 0.89, 1.11, 1.33, and 1.56 m/sec. Oxygen consumption during four minutes of standing rest was also collected.

The authors then used a three compartment model to examine metabolic cost. Compartment one accounted for the basal metabolic rate, compartment two for maintaining balance, and compartment three the metabolic cost associated with walking movements ($y = ax^2 + b$; $y = VO_2$, x = walking speed). Individual linear regression r^2 values ranged from 0.92 to 0.99 for all subjects $p < 0.05$).

The 80 year olds subjects had a significantly higher resting basal metabolic rate (BMR), metabolic cost of balance (20.5% greater; $p = 0.007$), and cost of walking (28.8% greater, $p<0.01$) than the 25 year olds (Appendix A). The 65 year olds only significantly differed from the 25 year olds in basal metabolism ($p < 0.05$). The investigators also found that, relative to the 25 year olds, VO_2 was higher in the 80 year olds at all speeds whereas it was higher for 65 year olds at only two speeds (1.33, $p = 0.03$; 1.56 m/sec, $p = 0.02$).

An alternate three compartment model substituted BMR with standing VO_2 so that compartment one became the metabolic cost of standing; compartment two became the metabolic cost of maintaining balance during walking (the difference between the VO_2 equivalent to the cost of balance maintenance and the VO_2 of standing); and compartment three remained the cost of walking movements (Values in Appendix A reflect the three compartment model). Gate was also examined using the gait instability index and the measure of stride-time variability. The investigators found that although octogenarians had a greater stride metabolic cost of walking and stride-time variability, gait instability index was not related to the increased cost of walking. They concluded that the elevated metabolic cost in these subjects is multifactorial, and that gait instability is not the main contributing factor.

Rather, the authors suggest that the higher energy cost associated with walking movements might be due to the knee extensors. Maximal knee extensor isometric strength was more correlated with the cost of walking at faster than at lower speeds; and a greater amount of type II fibers and greater force development at the knee extensors occurred at faster speeds.

Larish et al. (1988) also examined the speed-economy relationship of walking between older and younger adults in order to see if walking economy (represented by oxygen uptake in ml/kg/min at a given speed) decreased with age (Appendix A). Older adults (n=17) in the study were about 70.5 years old, and young adults (n=11) were about 25.6 years old.
All subjects were physically adults engaged in regular walking, jogging, bicycling, aerobic dance, and/or strength training activities. The investigators chose such a population in order to attribute any age-related discrepancies to biological aging rather than pathological conditions.

Subjects performed five minutes of steady-state walking at speeds of 0.54, 0.81, 1.07, 1.34, 1.61, and 1.88 m/sec. Oxygen consumption at self-selected walking speeds was also obtained. True to the proposed walking economy curve, energy cost per meter rose as speed decreased or increased from the most economical speeds. Self-selected walking speed fell within the economical range in 82% of subjects. The investigators found that the oxygen consumption values of older individuals were higher than those for younger individuals at each speed, which might be reflective of decreased muscular efficiency.

Cycling. In discussing cycling as a modality Ortega (2013) conceeds that some cycling studies do not suggest decreased muscular efficiency with age but have found similar (Babcock et al. 1992), or greater (Venturelli et al., 2012 and Wajngarten et al., 1994) efficiencies with age. Nonetheless, he notes that these studies are limited due to values derived from non-steady state exercise.

Bell & Ferguson. Alternatively, he cites a cycling study (Bell & Fergusson, 2009) (Appendix C) in which older women (n = 8; 70 ± 4 years) and younger women (n = 8; 25 ± 3 years) performed a protocol of six minute bouts of cycling at cadences of 45, 60, 75, and 90 rpm at 75% of ventilatory threshold. Subjects rested for one hour between each period. The study addressed the effect of temperature on net and mechanical efficiencies between older and younger women ; control and heated protocols were done on separate study days. The investigators found that the young subjects had greater net (27.5 ± 4%) and mechanical efficiencies (32.0 ± 3.1%) than older (22.4 ± 6.9% ; 30.2 ± 5.6%, respectively) subjects across pedaling speeds under the control condition, but p-values between groups were not given.

Hopker et al. Another relatively supportive study by Hopker et al. (2013) addressed the influence of training status, age, and muslce fiber type on cycling efficiency and endurance performance (Appendix C). Subjects consisted of 40 males. Twenty were young (18-30 years old) and twenty were older (50-74). In each group 10 were trained and 10 were untrained but physically active. Young trained subjects had a minimum of two years of competitive road racing or history of time trials while older trained individuals had at a training and racing history of at least 10 years.

All subjects performed six-minute submaximal cycling bouts at 100, 150, and 200 watts 50 and 60% of their maximal minute power (MMP, the highest average power output recorded over 60 seconds). At the same intensities, they performed the bouts at fixed cadences of 60 and 120 rpm. Subjects were given a three minute rest period between bouts, and trained participants performed an additional bout at 250 watts using their preffered cadence. On the third visit, trained subjects had a time trial in which they sustained the highest power output possible for an hour. Lastly, participants from each group had a muscle biopsy from the right lastus vateralis.

While a comprehensive examination of protocol results could not attribute efficiency differences to age alone, the study did offer results supportive of decreased efficiency for some protocols. Cycling efficiency was not different between groups at 100 watts, but when cycling at 150 watts there was a significant interaction between training status and age ($F_{(1,33)} = 4.39$, $p= 0.046$) which favored the young. Trained young cyclist also had a significantly higher efficiency than trained old cyclists when cycling at 200 watts (1.46% greater, $t= -3.66$, $p<0.01$).

No interaction was found for gross efficiency at the relative work rate of 50 and 60%. There was a significant effect for training status (50% MMP $Wald_i = 38.98$, $p < 0.01$; 60% MMP $Wald_i = 14.10$, $p < 0.01$) and age (50% MMP $Wald_i = 31.61$, $p < 0.01$; 60% MMP $Wald_i = 4.56$, $p = 0.03$).

There was a main effect for training status ($Wald_i$ = 29.83, p <0.01) when cycling at 60 rpm at 60% MMP, but not for age or interaction. Meanwhile, a significant main effect for training (but not age, $Wald_i$ = p < 0.047, p = 0.049) was observed for cycling at 60% MMP at 120 watts ($Wald_i$ = 10.46, p < 0.01). No significant interaction was oberved at this load ($Wald_i$ = 3.13, p<0.08). Irrespective of age, endurance performance was correlated with cycling efficiency at 60% MMP at 120 rpm (r = 0.57, p < 0.01). However, cycling efficiency during the performance trial was higher than at the 60% MMP at 120 rpm bout (mean intensity = 69.5% MMP; and the young had efficiency values of 19.6 ± 1.2% vs 16.6 ± 1.5% efficiency in old p <0.01). Trained older cyclists also had a lower efficiency than the trained young during the time trial (18.7 ± 0.9 vs. 20.2 ± 1.3%, p < 0.01) when mean endurance power output was counted as a covariate.

Work rate corrected data determined that differences in VO_2 (3.31 ± 0.18 vs. 3.11 ± 0.18; p<0.05) rather than RER accounted for differences in endurance performance efficiency between the trained older and younger men (mean RER values were 0.929 ± 0.05 vs. 0.927 ± 0.05, p=0.94), which may support Ortega's assertion that slower uptake kinetics in older adults result in decreased mechanical efficency. Hopker et al. stated that cycling efficiency decreases with age regardless of training status at relative work rates of 50 and 60% MMP (p < 0.05). When examining differences in trained cyclists, younger men had greater efficiencies than the older at both absolute and relative workrates (p < 0.05)

STUDIES IN SUPPORT OF INCREASED EFFICIENCY.

Venturelli and Richardson cite a cycling study they conducted which examined lung function, metabolic cost, and work rate in female centenarians (Venturelli, Schena, Scarsini, Muti, & Richardson, 2013) (Table 3). The study is noteworthy for the 80-year difference between the young (18-22 years; m = 21 ± 1; n = 8) and older (98-100 years; m = 100 ± 1; n = 8) subjects, and a dramatic increase in exercise economy in the old as compared to young: the costs of cycling at absolute work rates were lower for centenarians, who consumed 46% less oxygen than the younger women at the same absolute work rate (30 watts), despite the fact that they were performing exercise at maximal intensity at that work rate.

Exercise protocol on the cycle ergometers differed, but still allowed for absolute comparison. Young participants performed two graded exercise tests (GXT's). The first one progressed in one-minute increments of 15 watts, and the second one in one minute increments of 15% of maximum work. Older participants performed only one GXT which progressed in 5 watt increments every minute. Thus, combining the data from the two GXT's performed by the young "allow(ed) an absolute and relative work rate comparison between groups" (Venturelli et al., 2013).

Results should be interpreted with caution, however, as other differences are quite significant. For instance, lung function was significantly compromised in centenarians as compared to the young as illustrated by the ratio of forced expiratory volume in 1 second to total forced expiratory volume (young = 77 ± 5%; centenarians = 55 ± 10%). Centenarians also had a 50% greater dead space per tidal volume at all but their maximal intensities (wherein the young were performing a relatively low amount of work). Erythrocyte, hemoglobin, and iron levels all significantly differed in the young as compared to centenarians (young = 4.2 ± 0.02 10^6 μl^{-1}, centenarians= 13.6 ± 0.5 gdl^{-1}; young= 83± 10 $\mu g\ dl^{-1}$, centenarians = 3.5 ±0.3$10^6$ μl^{-1}; young= 11.1±1.2 gdl^{-1}, centenarians= 23 ± 1 $\mu g\ dl^{-1}$, respectively, $p<0.001$). The authors also report that although alveolar oxygen partial pressure (PO_2) was maintained in both groups during exercise, arterial PO_2 fell steadily in the centenarians to levels considered below normal for both groups (i.e. 3-4 ml/per watt; normal uptake ranges are 8-12 ml/watt). According to the authors, study findings imply that centenarians are able to compensate for limited oxygen transport via improved skeletal muscle efficiency.

FINDINGS MAY VARY DUE TO DIFFERENCES IN METHODOLOGY

A number of methodological differences may account for the variance in study findings. These include differences associated with senescence such as a decrease in muscular strength and altered fiber type, and altered exercise capacity. In addition, study findings may be influenced by subject fitness status, muscles examined, modalities utilized (walking vs. cycling), and differences in exercise protocols (Appendices A and C).

Differences in energy cost and efficiency equations (Appendices B and D) may also bear substantial influence on study results (Gaesser & Brooks, 1975). Other considerations are differences in subject genders and sample sizes (Appendices A and C).

Age and sarcopenia. Ages are essential to the altered economy/efficiency debate because the effects of sarcopenia and reductions in exercise capacity occur with and across differing "old" ages. For instance, sedentary persons lose an estimated 20-40% of their muscle mass through the course of their adult lives, and a loss of muscle mass occurs with senescence regardless of physical activity (Spirduso, Francis, and MacRae, 2005). Some observations demonstrate a decline in cross sectional muscle fiber area, fiber number, and changes in muscle quality as early as 40 years of age (Nair, 2005). After age 50, strength declines by 1% every year until age 70, when decrements reach 3% a year. Declines in muscle and locomotive performance are more prominent at 65 years and older (Skelton, Greig, Davies & Young, 1994, as cited by Bell & Ferguson, 2009), with the most profound effects of sarcopenia in locomotive muscles occurring after age 80 (Venturelli & Richardson 2013 cite Buford et al., 2012). An estimated 40% of those 80 and above are affected (Marzetti & Leewenburgh, 2006 cite Baumgartner et al., 1998). Thus, muscular strength may vary significantly between ages 50, 65, 70, and 80+.

Fiber type. In addition to overall decrements in muscular strength and mass, older muscle is relatively less powerful than younger muscle (Spirduso et al., 2005). This is due in part to the loss of type II fibers and atrophy of the remaining type II fibers. As mentioned previously, type II fibers have greater conduction velocities and are thus able to generate force more quickly than type I fibers. A comparative study by Hikida et al. found a 40% reduction in type II fibers in the quadriceps of men ages 58-78 (2000; cited by Spirduso *et al.*, 2005). Fiatarone-Singh et al. observed a 60% decrement in type II quadriceps muscles in men and women ages 72-98, with a 7% rise in type I fibers (1999; cited by Spirduso et al., 2005). Similarly, Hakkinen et al. found a 2% net gain of type I fibers in men aged 29-60 (1998; cited by Spirduso et al., 2005).

Type IIa fibers are often overlooked but should not be discounted as they are part of the fiber pool. These fibers contain high levels of both aerobic and anaerobic enzymes which allows them to utilize both types of energy transfer. They have an intermediate contraction speed and are known as fast-oxidative-glycolytic fibers. Anderson, Terzis and Kyger examined fiber distribution in twelve subjects ages 85-98 (88 ± 1) years old.

They found that Type I fibers accounted for 19.9 ± 3.3%; type IIa comprised 27.2 ± 5.8%; and 0.3 ± 0.3% of muscles were type IIx. The remaining 50% of fibers displayed a co-expression of one or more fiber types—a trait more readily seen in older muscle and relatively uncommon in young muscle. The colleagues found that fibers which co-expressed type I and IIa comprised 28.5 ± 5.9% of the fibers; those co-expressing IIa and IIx were 22.2 ± 4.7 %; and fibers co-expressing I and IIx made up 0.7 ±0.9 %. Therefore progressive changes in fiber type composition and co-experession may influence power, efficiency, and expenditure values. Intra-study comparisons between “old” age groups may potentially differ depending upon subject ages and fiber types.

Exercise capacity. Meanwhile, the decreased exercise capacity associated with senescence has ramifications for exercise testing in this population. Older adults have slower oxygen uptake kinetics and generate more energy via anaerobic glycolysis at the start of exercise than young adults (Babcock et al.,1992 ; Bell et al.,1999; and Chilibeck, Paterson, Smith, & Cunningham, 1999). At the same time, older adults may fatigue more quickly given the same absolute workrate as younger adults. As Venturelli and Richardson point out, this presents a challenge in developing test protocols for the "oldest of the old," i.e. centenarians: there is a trade-off between obtaining steady state values and reaching the highest levels of submaximal exercise attainable.

Influence of muscular adaptations and physical fitness. Because exercise capacity, gross and absolute energy expenditures, and exercise efficiencies tend to vary across fitness strata, study comparisons may be limited by differences physical activity and/or fitness status. For instance, Hopker et al. (2013) suggested that exercise training may have a confounding effect when addressing efficiency differences between young and older groups by altering fiber type. They conducted an exercise study (as previously described) which included muscle biopsies and the use of trained and untrained younger and older men to address potential differences in cycling efficiency in these groups. The authors found a higher amount of type I fibers in the trained as compared to the untrained ($p < 0.01$).

However, the amount of type I fibers did not vary between older and younger men, nor could it account for efficiency differences between age groups ($p<0.01$). Upon examining the results of various cycling protocols, the authors ultimately concluded that differences in cycling efficiency were not related to age or fiber type, but rather to the variation in training status. Thus, it is plausible that individual and cellular adaptations to exercise (e.g. increased mitochondrial enzymes) rather than mere fiber distribution influenced study results.

Increased efficiency associated with exercise (or a sufficient level of physical activity) is not unique to cycling protocols. Nor are the higher relative efficiency values of the trained compared to the untrained limited to young adults. In fact, exercise intervention studies suggest that the influence of fitness may be especially pronounced in sedentary older populations, who may derive greater benefits from exercise training than the sedentary young (Woo *et al.*, 2006). Thomas, De Vita, & Malacuso (2006) demonstrated an 18-21% percent increase in walking economy (as expressed by walking cost per unit of distance; 11 females, age = 79.6 ± 3.7 years) at slow, comfortable, and fast ground walking speeds after 12 weeks of high intensity interval treadmill training which featured weight unloading ($p < 0.05$). The exercisers also increased maximal walking speed by 12.6% ($p = 0.02$) and increased their mechanical power output at ventillary threshold by 67% ($p < 0.017$) relative to baseline levels.

Thus, even when comparing populations of the same age, efficiency values may drastically differ due to differences in physical fitness which may be influenced by favorable muscle fiber adaptations in response to exercise or physical activity levels sufficient to improve fitness. Comparative age group studies in which subject groups also differ in physical fitness status may be misleading due to potential confounding from the influence of fitness status.

Muscles Examined. Layec, Trinity, & Hart pointed out that age related alterations in muscle efficiency vary between muscle groups (2013). They note that Venturelli & Richardson's observation of improved metabolic efficiency was observed in the tibialis anterior, which appears to have preserved oxidative capacity and mitochondrial efficiency with increased age.
In contrast, the vastus lateralis appears to display reduced contractile and mitochondrial efficiencies with age. Age-related efficiency variance in these muscles as well as changes in their relative contributions to walking and cycling could conceivably influence study findings.

Modality. Thirdly, differential results across studies may be due to differences in exercise modality. While the majority of Ortega's supportive exercise studies involve walking, Venturelli & Richardson mainly cite cycling studies to support increased efficiency. It has been suggested that results may vary between the two modalities because walking is considered a complex task : individuals must balance, bear their own weight, processes visual input, and otherwise navigate the walking surface.

In the Larish et al. (1988) study , the authors hesitated to support decreased economy despite observing a higher oxygen uptake in older adults as compared to younger adults walking at the same speed. They reported that three older adults and two younger adults selected speeds outside of the economical range, which did not support decreased economy in older adults per se.

Older adults also selected the same preferred treadmill walking speeds as younger adults (1.21, 1.19 m/sec). Others have observed the same self-selected speeds for treadmill walking in older and younger individuals, but note that self-selected walking speeds for ground walking are consistently lower in older individuals (Allman & Rice, 2004).

This may be due to the assistance provided by the moving conveyor belt during the push off phase of walking. Although treadmill walking also circumvents navigation issues associated with ground walking, individuals must still maintain balance and expenditure values may still be influenced by differences in gait patterns. Thus, a greater degree of variability in work rate may occur even at standardized treadmill work rates as compared to those established using other modalities.

In contrast, cycle ergometry is a simple, stationary exercise for which subjects do not have to contend with weight-bearing, navigation, or lower-body balance. The use of foot straps may serve to direct and increase the coupling of muscular work to the production of mechanical work. Moreover, the use of both pedaling cadence and cycle load to determine work rate gives the investigator a greater degree of control and precision in setting standardized work rates. This likely results in a lesser degree of work rate variance between subjects performing at the same standardized work rate.

Calculations. Importantly, efficiency calculations and expressions of energy expenditure vary among studies (Appendices B and D). These differences make intra-study comparisons and inferences less straight-forward. Gaesser & Brooks demonstrated this in comparing efficiency calculations for cycle ergometry at various speeds (1975).

Calculation comparisons included those for gross, net, work, and delta efficiencies. Gross efficiency is the ratio of work accomplished to energy expended (multiplied by 100). Net efficiency is calculated the same way, except that resting energy expenditure is subtracted from total energy expenditure. In the work efficiency calculation the denominator becomes “energy expended above that in cycling without a load” (total energy expenditure – unloaded cycling energy expenditure). Finally, delta efficiency is the ratio of delta work accomplished to delta energy expended. The investigators used these in examining steady-state cycling efficiency across work rates (0, 200, 400, and 600 kg/m*min) at each of the following cadences: 40, 60, 80, and 100 rpm.

The work efficiency calculation proved challenging because obtaining zero-work equivalents was difficult. The authors used the y-intercept of the work rate regression in lieu of zero work values. Initially, it appeared efficiency increased with pedaling cadence under gross and net efficiency calculations. However, because the baseline VO_2 (i.e. resting VO_2) in the denominator does not approximate the y intercept of the VO_2 in the VO_2-work rate regression, it appears that VO_2 values at higher work rates are proportionately less than those at lower work rates.

In other words, when lower work rates are used in the equation, the denominator is relatively larger because the lower work rate is closer to resting energy expenditure. In contrast, a higher work rate decreases the denominator, which yields a larger percentage. Thus, the appearance of efficiency values increasing with speed was deemed a calculation artifact. Since the delta equation takes into account the changes between baseline and each speed as well as changes in expenditure at any point along the regression, changes in work rate are represented in the efficiency estimate. It has been determined the most accurate calculation for estimating muscular efficiency. However, when only one work rate is available, gross and net (rather than delta) calculations are considered suitable for examining efficiency.

Lastly, varying inter- and intra-study subject gender may or may not influence metabolic costs or efficiency findings (Mian *et al.*, 2006). It has also been suggested that some studies do not demonstrate anticipated findings due to low statistical power associated with an insufficient subject pool (Coyle et al., 1992).

In conclusion, exercise study findings may vary due to: variances in sarcopenia and altered fiber type with age, altered exercise capacity in senescence, the influence of fitness status, muscle groups examined, exercise modality utilized, exercise protocol, and differences in energy cost and efficiency equations. Subject genders and sample sizes also vary. Additional studies which compare differences across segments of “older” populations are needed to address differences associated with the first three factors listed. Comparative modality studies (using matched steady-state submaximal work rates) and studies which aren’t limited by gender or sample size may also be beneficial.

CHAPTER 3

METHODS

SUBJECTS

Subjects consisted of 207 (walking) and 237 (cycling) adults who were recruited as part of a National Institute of Health (NIH)-funded study to develop and validate a wireless, multi-mode neural network-based physical activity/heart rate monitor (Appendix E). Individual ages ranged from 18-81 years old. All subjects were healthy and free of orthopedic or mobility problems. Each had a fitness level sufficient to perform 90 minutes of various activities of daily living including walking (treadmill based) and submaximal cycling (cycle ergometer). Subjects performing treadmill walking consisted of 86 young adults (44 male; 42 female) aged 29.6 ± 10.5 years, and 121 older adults aged 66.8 ± 4.5 years (72 male; 49 female). Subjects performing cycle ergometry consisted of 116 young adults (43 male, 73 female) aged 29 ±10 years and 121 older adults (72 male, 49 female) aged 67 ± 4 years. Individuals between the ages of 18-59 years old were qualified as young adults; those 60 years old and older were considered older adults.

PROCEDURE

Calorimic walking values were collected from eight minutes of level treadmill walking on a TMX425C Trackmaster treadmill (Full Vision Inc., San Diego, CA, Newton, KS.) at three miles per hour (1.34 meters per second). Cycling values were collected from eight minutes of cycle ergometry performed on a Monark Ergomedic 828 E electrically braked cycle ergometer (Monark Exercise AB., Kroons väg 1, Sweden) at 50 watts (pedaling cadence 60-70 rpm). Values from eight minutes of seated and standing rest were also obtained (standing rest values were used in walking calculations, and seated rest values were used in cycling calculations). Subjects also rested for four minutes between each activity to allow the heart rate to return to resting levels. Oxygen uptake (milliliters per minute) during rest and each activity was measured utilizing the CareFusion Oxycon Mobile Device (San Diego, CA.).

Thirty second breath-by-breath averages were used to obtain the average oxygen uptake during the last five minutes of each activity. Subject data used in statistical analysis demonstrated a plateau in VO_2 during the last five minutes of activity and RER values <1.0. Thus, only steady-state submaximal work values were included in the analysis.

MEASURES AND ECONOMY / EFFICIENCY CALCULATIONS

Study measures for both walking and cycling included gross and net oxygen consumption values and gross and net caloric expenditures (calculated using respiratory exchange ratios). Net values were derived by taking resting values from activity values. Walking economy was represented by gross caloric expenditure (kcal/kg/min) and net caloric expenditure (walking kcal/kg/min - resting kcal/kg/min).Cycling measures included gross and net cycling efficiency values; which were multiplied by 100 to be expressed as a percent. Gross cycling efficiency was the dividend of the caloric equivalent of 50 watts (0.717 kilocalories) divided by the individual's gross caloric expenditure cycling at that work rate. The value was then multiplied by 100 to express efficiency differences in terms of percent:

Gross efficiency = 0.717 / cycling caloric expenditure (1)

A similar equation was used to calculate net efficiency, which was also multiplied by 100 to be expressed as a percent. The 0.717 caloric equivalent of 50 watts was used in the numerator, but this time net (rather than total) caloric expenditure was used for in denominator:

Net efficiency = 0.717 / (cycling caloric expenditure – resting caloric expenditure) (2)

STATISTICAL ANALYSIS

Baseline comparisons. Baseline anthropometric characteristics (height mass, percent body fat), between young and older adults using independent t-tests (Appendix E).

Linear regressions. Linear regressions were performed to assess oxygen uptake (walking = ml/kg/min; cycling = ml/min), net oxygen uptake (walking= ml/kg/min; cycling= ml/min), caloric expenditure (walking= kcal/kg/min; cycling= kcal/min), net caloric expenditure (walking= kcal/kg/min; cycling = kcal/min), and gross and net efficiencies (cycling only) (percentages derived from kilocalories), as a function of age for each modality (Appendix A, Appendices H-K for walking graphs and Appendices L-Q for cycling).

Independent t-tests. Unpaired t-tests were used to assess differences in means between young and older subjects for each measure, as listed above, (oxygen uptake, net oxygen uptake, caloric expenditure, net caloric expenditure, and gross and net cycling efficiencies) for each modality (α= 0.05) (Appendix G).

HYPOTHESIS

Since activities were done at a low submaximal intensity and increased contractile efficiency may compensate for age-related mitochondrial deficits, I hypothesize that there will be no impact of age on walking economy and cycling efficiency.

CHAPTER 4

RESULTS

The VO_2 and energy costs for each modality in younger vs. older participants are presented in Appendix F. Linear regressions were conducted to examine gross and net energy costs (cycling and walking), and gross and net efficiencies (cycling), as a function of age. Regression results are included in Appendix G. Scatterplots showing the lines of regression are presented in Appendices H-K (walking) and L-Q (cycling). Independent T-tests were used to compare efficiencies and economies by age; p values are included in Appendix G.

SUBJECTS

Walking. Subjects who performed level treadmill walking consisted of 116 young (M=44; F=42) and 92 older (M=92; F=49) adults (Appendix E). Young walking subjects were aged 29.60 ± 10.50 years and older ones were 66.80 ± 4.50 years old (p value for mean age variation= 0.000). There were no significant differences in height between groups (younger=168.90± 9.8 cm; older= 168.60 ± 8.60 cm; p=.878). Subjects significantly differed in body mass (younger=70.70 ± 15.90 kg; older=75.90 ± 16.80 kg; p=0.029) and percent body fat (younger= 25.80 ± 8.80%; older= 32.40 ± 8.80%; p<0.001).

Cycling. Subjects performing cycle ergometry were 116 young (M=43; F=73) and 92 older (M=38; F= 54) adults (Appendix E). Younger subjects were 29.00 ± 4.00 while older subjects were 67.10 ± 4.00 years old. Subjects did not significantly differ in height (young= 168.80 ± 10.00 cm; older=78.00 ± 8.50 cm; p= 0.318). Subjects again significantly differed in body mass (young= 70.80 ± 16.00 kg; older= 78.00 ± 16.60 kg; p=0.002) and percent body fat (young= 25.90 ±10.70%; older= 32.80 ± 8.90%; p<0.001).

WALKING ANALYSIS.

Linear regressions. Linear regressions revealed no statistically significant relationship between age and gross VO_2 (β= -0.121; $R^{2=}$ 0.015; p = 0.083), gross kilocalorie expenditure (β= -0.093; R^2=0.009; p = 0.183), net VO_2 (β= 0.115; R^2= 0.013; p=0.099) or net kilocalorie expenditure (β= 0.088; R^2= 0.008; p=0.205) (Appendix F; graphs in Appendices H-K).

Independent t-test Results confirmed that there were no significant differences in gross VO_2 (ml/kg/min) (young = 12.66 ± 1.52 ml/kg/min; older = 12.28 ± 1.63 ml/kg/min; p = 0.069), net VO_2 (young = 8.63 ±1.25 ml/kg/min; older = 8.89 ± 1.52 ml/kg/min; p = 0.222), gross energy expenditure (young = 0.0615 ± 0.00786 kcal/kg/min; older = 0.0599 ± 0.00876 kcal/kg/min; p=0.122) or net energy expenditure (young = 0.0425 ± 0.00686 kcal/kg/min; older = 0.0435 ± 0.00794 kcal/kg/min; p = 0.336) between age groups (Appendix G).

CYCLING ANALYSIS.

Linear regressions. Linear regressions (Appendix F) show a statistically significant decrease in gross VO_2 with age (β = -0.167; R^2 = 0.028; p = 0.016), and a trend for a decrease in net VO_2 with age (β = -0.135; R^2 = 0.018; p = 0.051). Gross energy expenditure was also significantly correlated with age (β = -0.156; R^2 = 0.024; p = 0.024), but net energy expenditure was not (β = -0.117; R^2 = 0.014; p = 0.091). Gross efficiency was significantly correlated with age (β = 0.168; R^2 =0.028; p = 0.015) and a trend was found for net efficiency (β = 0.128; R^2 = 0.016; p = 0.064). Despite statistically significant regression coefficients, an extremely low percentage of the variance in VO_2, energy expenditure, or efficiency was explained by age (< 3%).

Independent T-tests. Independent T-tests (Appendix G) for cycling indicate significant differences in gross VO_2 (young = 909.10 ± 125.70 ml/min; older = 863.40 ± 137.50 ml/min; p=0.006), gross caloric expenditure (young= 4.513 ± 0.600 kcal/min; older = 4.304 ± 0.700 kcal/min; p=0.007), and net VO_2 (young = 619.02 ± 91.34 ml/min; older = 596.21 ± 107.60 ml/min; p = 0.046) between age groups. There was no significant difference between groups for net caloric expenditure (young = 3.090 ± 0.446 kcal/kg/min; older = 2.990 ± 0.541 kcal/kg/min; p=0.053). Gross efficiency was statistically significant between groups (young = 16.20 ± 2.30%; older = 17.06 ± 2.60%; p = 0.007); and net efficiency differences were statistically insignificant between groups (young = 23.80 ± 4.00%; older = 24.80 ± 4.60%; p = 0.054).

CHAPTER 5

DISCUSSION

WALKING

The findings of the present study (Appendix G) are consistent with the results of Malatesta *et al.* (2003) who reported no significant differences in walking economy between young subjects and older subjects ages 65.3 ± 2.5 years old across speeds (0.67-1.56 m/sec). The Malatesta et al. study (2003) most closely resembled the present one in subject ages (young = 24.6 ± 2.6 years old & old= 65.3 ± 2.5 years old, vs. young = 29.6 ± 10.5 years old & older = 67.10 ± 4.0 years old, respectively) and economy calculations (VO_2 ml/kg*min/m*sec vs. VO_2 ml/kg/min - resting VO_2 ml/kg/min, respectively; Appendices A and B).

Similarly, Larish et al. (1988) concluded no difference in walking economy with age (Table 1). The authors used gross walking oxygen consumption (ml/kg/min) as a “measure” of economy; these values were given relevance when plotted against speed (m/sec). The investigators found that the preferred walking speed (i.e. the self-selected pace when no set speed was given) chosen by 18% of subjects (three old and two young; p value not given) fell outside of both the range of proposed optimal economy, which didn’t support the notion that older adults (per se) have reduced economy. While VO_2 increased with age, both young and older individuals had the lowest levels of oxygen consumption at the same speeds (1.07-134 m/sec) (p value not given).

The “speed for optimal economy” proposed by Larish et al. (1.07-134 m/sec) corresponded to that used in the present study (1.34 m/sec), which also indicated no significant difference in walking economy between younger and older individuals (gross energy expenditure: y= 0.062 ± 0.008 kcal/kg/min, o = 0.060 ± 0.009; p= 0.122; net energy expenditure y = 0.040 ± 0.007 kcal/kg/min, o= 0.044 ± 0.008 kcal/kg/min; p= 0.336). Thus, the present study supports Larish et al.’s findings even though the former used net caloric expenditure (Resting kcal/kg/min subtracted from gross walking kcal/kg/m) as opposed to gross oxygen consumption (ml/kg/min) to express walking economy (Appendix B).

The present findings are not supported by other studies (Ortega and Farley, 2007; Woo et al., 2006; Mian et al., 2006) which suggest that walking economy decreases with age. Again, these studies use different measures of economy (Appendix B). Hortobagyi et al. (2011) converted net VO_2 (exercise VO2-resting VO2) to joules/kilogram/second and then divided it by walking speed (m/sec). Ortega and Farely (2007) and Mian et al. (2006) did the same. The calculation used by Woo et al., 2006 involved further conversions: Percent efficiency = 1,435, the constant to convert given watts to Kcal÷ [(3,840 kcal + 1,180 * RER)* Walking VO_2/ Watts]. These expressions of economy differed from those of the present study to a greater extent than those used by Malatesta et al. (2003) and Larish et al. (1988) (Appendix B).

In order to obtain a more objective comparison between the present study and those cited herein, an effort was made to convert values from each study to obtain VO_2 values obtained at or near at 1.34 m/sec (or given speeds which were closest to 1.34 m/sec). However, because not all studies reported mean VO_2 values, this was not feasible. Caloric expenditure could not be used either for the same reason and a lack of RER values. Future studies which report such values could further aid investigators in interpreting study results.

A second factor is the cause of the debate itself: the notion that economy (and efficiency) differences are attributable to physiological alterations occurring as a function of older age. The ages of the older subjects in studies supporting age-related decrements in economy (Hortobagi et al., 2011; Ortega and Farley, 2007; Mian et al., 2006; and Malatesta et al., 2003,) are greater than the ages of older individuals in the present study (Appendix A).

In these studies mean subject ages of older individuals range from 74 to 81 years old, whereas the mean older age of the present study was 67 years old. The Malatesta et al. study was unique both in including octogenarians (n=10), and in separating them from those in their mid- to late sixties (n=10) (2003).

While results of subjects in their mid-to late sixties (O_1) did not differ from those of the present study (i.e. no difference with age), octogenarians in their study had reductions in efficiency as compared to both young subjects in the present study (m ~ 30 years) as well as those in their young group (m ~ 25 years) ($p < 0.01$) (Appendix A).

It has been suggested that muscular strength declines by 1% every year until age 70, when decrements reach 3% a year (Spirduso et al., 2005); and the most profound effects of sarcopenia in locomotive muscles occur after age 80 (Venturelli & Richardson 2013, cite Buford et al., 2012). Separate studies performed by Conley and colleagues suggest that reduced maximal ATP generation and reduced maximal power output affect work efficiency (Conley *et al.*, 2000a, & Conley *et al.*, 2000b, cited by Conley, Jubrias, Cress and Esselman, 2012). The colleagues attribute these alterations to decreased mitochondrial content and loss in total muscle mass (respectively) in senescence.

Subsequent work by Conley and others included a comparison of muscular efficiency, mitochondria coupling efficiency, maximal ATP production, contractile efficiency (i.e. muscular work generated per unit of ATP), and maximal power output and between young and older adults (2012). Relative declines in both maximal power output and maximal ATP generation were seen in older adults but means for contractile coupling efficiency were small and did not statistically differ between age groups (younger = 0.05 ± 0.04; older = 0.58 ± 0.04; $p > 0.05$). Contractile coupling efficiency ($\varepsilon_{c)}$ trended toward an *increase* for older as compared to younger adults (older ε_c~ 0.59; younger ε_c~ 0.59; $p > 0.05$). The authors note that the values are corroborated by calulations by Whipp & Wasserman, 1996; Gaesser & Brooks, 1975; and direct calorimetric values by Krustrup, et al., 2003. Increased contractile efficiency is also consistent with a prevalence of type I fibers due to sarcopenia in older muscle (Coyle et al., 2012).

The same was not true for mitochondrial coupling, which was strong in the young (0.58 ± 0.08; optimal mitochondrial coupling efficiency = 0.60) but was lower in older adults (0.44±0.03) ($p < 0.05$). Furthermore, a decline in percent delta cycling efficiency in older individuals in the absence of reduced contractile efficiency implies a decrement in mitochondrial coupling efficiency. Thus, results suggest that compromised mitochondrial coupling rather than contractile coupling efficiency results in the decline of muscular efficiency and maximal power output in older adults.

Although power output results of the study were elicited from cycle rather than walking work, the former is likely a better indicator of muscular power because it eliminates cofounders such as differences in gait and balance. Biochemical factors may affect internal work that contributes to variation in energy cost during walking in general, or as a function of age. In the current study no assessments were made of biomechanical/ gait differences that might have differed between the young and older subjects. However, inspection of Appendix G or Appendices H and L indicates a similar variation in VO_2 among both young and older subjects. If the inter-subject variation in energy expenditure is due to biomechanical factors, the present data suggest that these factors are not necessarily age dependent.

CYCLING

Stationary cycle ergometry, unlike level-grade treadmill walking, is more useful for determining whether there are age-related differences in muscular efficiency. This is because work rate (and, therefore, work accomplished in a fixed amount of time) can be accurately measured on the cycle ergometer. If pedaling cadence is controlled, as it was in this study, then the energy expenditure derived from VO_2 can be used to assess the energy cost of the work accomplished. One caveat is that some of the VO_2 represents the energy cost not only of non-exercising tissues, but also of the energy cost of moving the limbs without a load. The most appropriate definition of muscular efficiency is the “delta” efficiency.

The delta efficiency is essentially defined by the inverse of the slope of the VO_2-work rate relationship, and thus can be used to subtract the "y-intercept" from the gross exercise VO_2 in order to effectively eliminate the VO_2 due to non-exercising tissue as well as that of unloaded cycling (Gaesser & Brooks, 1975). Due to the design of this study, it was not possible to obtain the slope of the VO_2-work rate relationship, nor was it possible to obtain the y-intercept.

The net efficiency definition comes closest, and, by eliminating the resting metabolism from the energy cost of exercise, can be used to compare the "net" energy expenditure for a given subject. This may not reflect true muscular efficiency, but it can serve as the "next best" estimate of the energy cost of the working muscles.

In this regard, the results of the current data suggest that older individuals may have slightly greater cycle ergometer efficiency than their younger counterparts. Gross cycling efficiency in older persons (17.10 ± 2.60%) was greater compared to younger persons (16.20 ± 2.30%) ($p = 0.007$), and there was a trend ($p = 0.054$) for net cycle ergometer efficiency to be greater in older adults (24.80 ± 4.60%) than young adults (23.80 ± 4.00%). This conclusion must be interpreted with caution, however, because net efficiency is not the best measure of muscular efficiency (Gaesser & Brooks, 1975). Our results are, however, in support of the only study cited herein which supports increased cycling efficiency in older individuals (Venturelli *et al.*, 2013).

Additionally, the statistical significance of our study does not necessarily mean the differences have practical or clinical relevance. The results of the study by Venturelli and colleagues may be misleading due to methodology. Oxygen consumption values were derived from a single minute of exercise data from a graded test utilizing two minutes per stage. Because it generally takes two to three full minutes for an individual to reach steady-state, this approach likely underestimates metabolic energy consumption while overestimating efficiency.

Furthermore, the VO_2-work rate slope of the older subjects used in the study by Venturelli et al is an unphysiologically low ~3-4 ml O_2/min per watt. Most studies indicate a slope in the range of ~8-12 ml O_2/min per watt.

The effect may be further magnified in older adults, who have relatively slower oxygen uptake kinetics and may take longer to reach metabolic steady-state (Ortega, 2013). While Hopker et al. (2013) report decreased efficiency with age, the same reservation applies to their study as VO_2 efficiency values were also derived from a single minute of exercise (2013).

CHAPTER 6

CONCLUSION AND APPLICATIONS

One limitation of the present study is that for each exercise modality one exercise load was used. A more robust design would have included multiple walking speeds and several work rates on the cycle ergometer that would have allowed for a better characterization of the relationship between VO_2 and either walking speed or work rate for each individual.
The use of multiple work rates is preferable because it allows efficiency to be examined at each and as a function of work rate. Multiple work rates also provide more data points by which to compare the efficiency slopes between age groups, and they allow more precise efficiency calculations to be used (i.e. delta efficiency as opposed to gross and net efficiencies).

In conclusion, the findings of the present study do not support altered walking economy with age (young = 0.040 ± 0.007 kcal/kg/min; older = 0.044 ± 0.008 kcal/kg/min p=0.336). Gross cycling efficiency was higher in older subjects (younger = 16.20 ± 2.30%; older = 17.10 ± 2.60% p=0.007), and a trend was observed for higher net efficiency (younger = 23.80 ± 4.00; older= 24.8 ± 4.60, p = 0.054). Since the net efficiency eliminated the contribution of resting metabolism, but not necessarily the energy cost of moving the limbs without a load, it remains to be established whether muscular efficiency is truly higher in older subjects. Future studies may contribute an even dispersion between subject ages and genders; incorporate multiple matched work rates between modalities; and utilize delta rather than gross or net efficiency calculations.

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APPENDIX A

COMPARISON OF WALKING STUDIES

APPENDIX A

COMPARISON OF WALKING STUDIES

Table 1

Walking Study Characteristics

Study	N	Sex	Ages	SS	Speed m/sec	AL	Finding
Hortobagi *et al.*, 2011	20 Y=10 O=10	M/F	Y=20.8± 2.0 O=77.4± 4.8	Y	.98	N/G	↓19.2% p=0.010
Ortega & Farley, 2007	20 Y=10 O=10	N/G	Y=27± 3 O=74± 4	Y	0.7-1.6	N/G	↓20% p=0.010 across speeds
Woo *et al.*, 2006	59 Y=25 O=34	M/F	Y=20-33 O=65-79	N	3.5	N/G	↓1.9% p<0.0001
Mian *et al.*, 2006	32 Y=12 O=20	M	Y=26.6± 3.3 O=74± 3.4	Y	.83-1.67	S	↓31% p<0.01 across speeds
Malatesta *et al.*, 2003	30 Y=10 O_1=10 O_2=10	M/F	Y=24.6±2.6 O_1=65.3±2.5 O_2=81.6±3.3	N/G	.67-1.56	N/G	↓ Y vs. O_2 p<0.01
Larish *et al.*	28 Y=17 O=11	N/G	Y= 25.6 O=70.5	Y	.81-1.88	PA	↔ p=N/G

Ages are reported as means ± SD; All values significant at .05
Findings are differences in economy of older relative to young; see table 2 for study economy measures and calculations.
N=Number O= Older; Y= Young; M=Male; F=Female
SS= Steady state; AL= Activity level; S=Sedentary; PA= Physically active
N/G= Not given

APPENDIX B

COMPARISON OF ECONOMY CALCULATIONS IN WALKING STUDIES

APPENDIX B

COMPARISON OF ECONOMY CALCULATIONS IN WALKING STUDIES

Table 2

Walking Study Economy Calculations

Study	Expression of Economy	Calculation	Finding
Hortobagyi *et al.* 2011	Cost of Walking	Walking VO2 – Standing VO2→ (Joules/kilogram^{-1}/second^{-1}) ÷ (speed in meters/second)	↓ Cost 19.2 Greater in O p=0.010
Ortega & Farley, 2007	Net metabolic cost of transport	Walking VO2 – Standing VO2→ (Joules/kilogram^{-1}/second^{-1}) ÷ (speed in meters/second)	↓ Cost 20% greater in O Across speeds p= 0.01
Woo *et al.*, 2006	Net metabolic cost of transport (Net VO2)	Walking VO2 (ml/kg/min) – Resting VO2 (ml/kg/min)	↓ Cost 1.9% greater in O P < 0.0001
	Percent efficiency *(Not given in table 1)*	1,435 constant for watts to Kcal÷ [(3,840 kcal + 1,180 * RER) * Walking VO2 / Watt]	↓ 3.6% less in O p < 0.000
Mian *et al.*, 2006	Cost of walking	Net energy expenditure/ speed expressed as joules/m*sec	↓ Cost 31%> in O across speeds p < 0.01
Malatesta *et al.*, 2003	The metabolic cost of walking	Walking VO2 (ml/kg/min) ÷ Speed (m/sec)	↓ Y vs. O_2 p < 0.01
Larish *et al.*, year unknown	Walking VO2	VO2 (ml*kg*m) ÷ Speed (m/sec)	↔ p= N/G Most economic speed for Y equals that for O

APPENDIX C

COMPARISON OF CYCLING STUDIES

APPENDIX C

COMPARISON OF CYCLING STUDIES

Table 3

Cycling Study Characteristics

Study	N	Sex	Ages	SS	Speed m/sec	AL	Finding
Hopker *et al.*, 2013	40 Y = 20 O = 20 10T/10U per age group	M	TY = 22 ± 3 UY = 27 ± 4 TO = 58 ± 8 UO = 58 ± 8	N	50-60% MMP 60 &120 rpm	T& U but PA	↓ Irrespective Of TS $p<0.01$
					1 hour Time Trial	T	~1% ↓ TO (vs TY) $p < 0.01$
Venturelli *et al.* 2012	16 Y = 8 O = 8	F	Y = 21 ± 1 O = 100 ± 1	N	GXT Up to 50 Watts	PA (Y) S (O)	↑ 46% lower cost across work rates
Bell & Ferguson 2009	16 Y = 8 O = 8	F	Y = 24 ±3 O = 74 ±4	Y	75% T_{vent} 45, 60, 75, & 90 rpm	PA	↓ % Net and Mechanical efficiency Across speeds $p < 0.05$

Ages are reported as means ± SD; All values significant at .05
Findings are differences in efficiency of older relative to young; see table for study efficiency measures and calculations
N=Number O= Older; Y= Young; M=Male; F=Female
SS= Steady state; AL= Activity level; S=Sedentary; PA= Physically active; T= Trained; U= Untrained
N/G= Not given

APPENDIX D

COMPARISON OF EFFICIENCY CALCULATIONS IN CYCLING STUDIES

APPENDIX D

COMPARISON OF EFFICIENCY CALCULATIONS IN CYCLING STUDIES

Table 4

Cycling Study Efficiency Calculations

Study	Expression of Efficiency	Calculation	Finding
Hopker et al., 2013	Percent Efficiency	Cycling kcal/ watts	↓ Irrespective of TS $p < 0.01$ 50-60% MMP
			~1%↓TO (vs TY) $p < 0.01$
Venturelli et al., 2012	Metabolic Cost	VO2 ml*min	↑ Across watts
Bell & Fergusson 2009	Percent Net Efficiency	Watts→ kJ/min ÷ Net VO2→kJ/min	↓ Across speeds Y=27.5 ± 4% O=22.4 ± 6.9% $p < 0.05$
	Percent Mechanical Efficiency	Internal + external power in watts→kJ/min ÷ kJ/min	↓ Across speeds Y= 32 ± 3.1% O=30.2 ± 5.6% $p < 0.05$

APPENDIX E

SUBJECT CHARACTERISTICS IN THE YOUNG AND OLD

APPENDIX E

SUBJECT CHARACTERISTICS IN THE YOUNG AND OLD

Table 5.

Subject Characteristics by Age

Walking	Subject Number	Age (Years)	Height (cm)	Mass (kg)	Body Fat (%)
	Young N=116 M= 44 F=42	29.60 ± 10.50	168.90 ± 9.90	70.70 ± 15.90	25.80 ± 8.80
	Older N=92 M=72 F=49	66.80 ± 4.50	168.60 ± 8.60	75.90 ± 16.80	32.40 ± 8.80
	Mean differences	p = 0.000	p = 0.878	p = 0.029	p = 0.002
Cycling	Subject Number	Ages (Years)	Height (cm)	Mass (kg)	Body Fat (%)
	Young N=116 M= 44 F=42	29.00 ± 4.00	168.80 ± 10.00	70.80 ± 16.00	25.90 ± 10.70
	Older N=92 M=72 F=49	67.10 ± 4.00	169.6 ± 8.50	78.00 ± 16.60	32.80 ± 8.90
	Mean differences	p = 0.000	p = 0.318	p = 0.002	p = 0.000

APPENDIX F

LINEAR REGRESSION COEFFICIENTS

APPENDIX F

LINEAR REGRESSION COEFFICIENTS

Table 6

Walking and Cycling Linear Regression Coefficients

		VO_2 ml/kg/min	Net VO_2 ml/kg/min	Kcal kg/min	Net Kcal kg/min	Gross Efficiency %	Net Efficiency %
Walking	β	-0.121	0.115	-0.093	0.088	-	-
	R^2	0.015	0.013	0.009	0.008	-	-
	Sig	0.083	0.099	0.183	0.205	-	-
		VO_2 ml/min	Net VO_2 ml/min	Kcal per min	Net Kcal per min	Gross Efficiency %	Net Efficiency %
Cycling	β	-0.167	-0.135	-0.156	-0.117	0.168	0.128
	R^2	0.028	0.018	0.024	0.014	0.028	0.016
	Sig	0.016	0.510	0.024	0.091	0.015	0.064

APPENDIX G

COMPARISON OF COSTS AND ECONOMY/ EFFICIENCY VALUES IN THE YOUNG AND OLD

APPENDIX G

ACTIVITY COSTS AND ECONOMY/EFFICIENCY VALUES BY AGE

Table 7

Activity Costs and Economy/Efficiency Values by Age

		Gross VO_2 ml/kg/min	Net VO_2 ml/kg/min	Kcal kg/min	Net Kcal kg/min	Gross Efficiency (%)	Net Efficiency (%)
Walking	Young N=115	12.70 ± 1.50	8.60 ± 1.30	0.062 ± 0.008	0.040 ± 0.007	-	-
	Older N=91	12.30 ± 1.60	8.90 ± 1.50	0.060 ± 0.009	0.044 ± 0.008	-	-
	Mean Differences	p = 0.069	p = 0.222	p = 0.122	p = 0.336	-	-
		Gross VO_2 ml/min	Net VO_2 ml/min	Kcal per min	Net Kcal per min	Gross Efficiency %	Net Efficiency %
Cycling	Young N= 117	909.10 ± 125.70	619.00 ± 91.40	4.513 ± 0.600	3.090 ± 0.446	16.20 ± 2.30	23.80 ± 4.00
	Older N=92	863.40 ± 137.50	596.20 ± 107.60	4.304 ± 0.700	2.990 ± 0.541	17.10 ± 2.60	24.80 ± 4.60
	Mean Differences	p = 0.006	p = 0.046	p = 0.007	p = 0.053	p = 0.007	p = 0.054

APPENDIX H

THE RELATIONSHIP BETWEEN GROSS WALKING OXYGEN UPTAKE AND AGE

APPENDIX H

THE RELATIONSHIP BETWEEN GROSS WALKING OXYGEN UPTAKE AND AGE

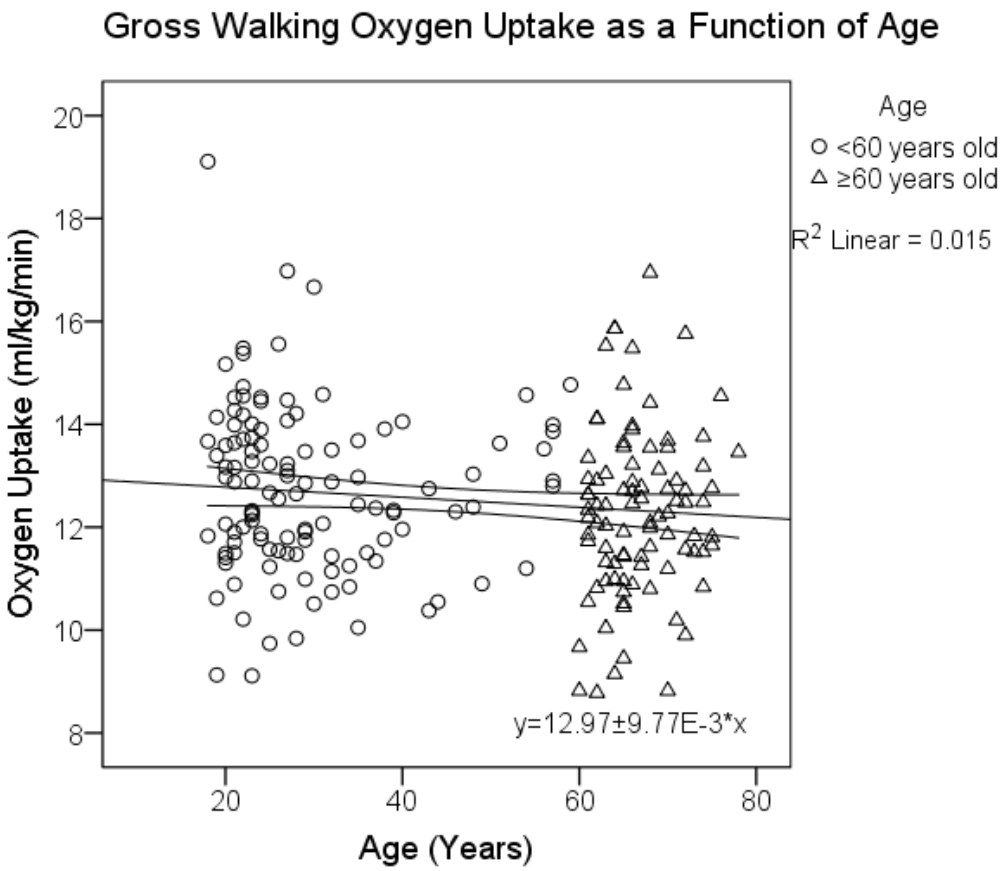

Figure 1. Scatterplot graph showing the relationship between gross oxygen uptake (ml/kg/min) in adults < 60 years old (circles) and ≥ 60 years old (triangles). Values are means from the last five minutes of treadmill walking at 3 mph (1.34 m/sec).

APPENDIX I

THE RELATIONSHIP BETWEEN NET WALKING OXYGEN UPTAKE AND AGE

APPENDIX I

THE RELATIONSHIP BETWEEN WALKING NET OXYGEN UPTAKE AND AGE

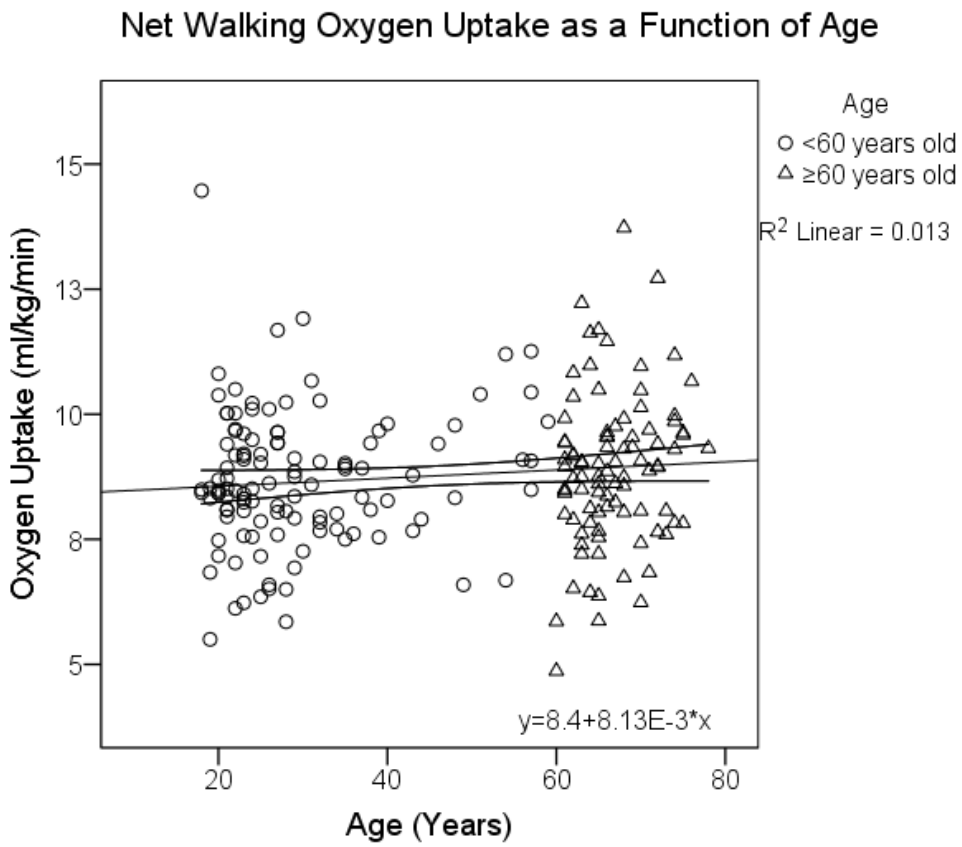

Figure 2. Scatterplot graph showing the relationship between net oxygen uptake (ml/kg/min) in adults < 60 years old (circles) and ≥ 60 years old (triangles). Net oxygen uptake = walking oxygen uptake – resting oxygen uptake. Values are means from the last five minutes of treadmill walking at 3 mph (1.34 m/sec).

APPENDIX J

THE RELATIONSHIP BETWEEN GROSS COST OF WALKING AND AGE

APPENDIX J

THE RELATIONSHIP BETWEEN GROSS COST OF WALKING AND AGE

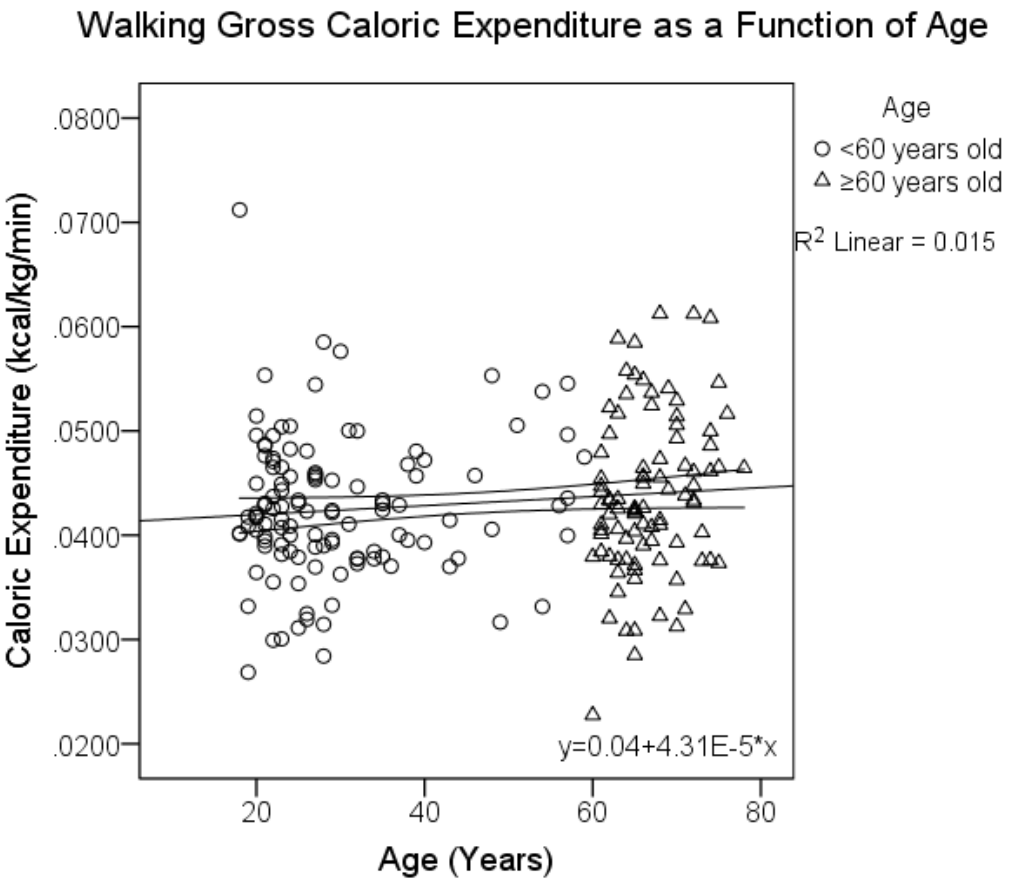

Figure 3. Scatterplot graph showing the relationship between gross caloric expenditure (kals/kg/min) in adults < 60 years old (circles) and ≥ 60 years old (triangles). Values are caloric means from the last five minutes of walking at 3 mph (1.34 m/sec).

APPENDIX K

THE RELATIONSHIP BETWEEN NET COST OF WALKING AND AGE

APPENDIX K

THE RELATIONSHIP BETWEEN NET COST OF WALKING AND AGE

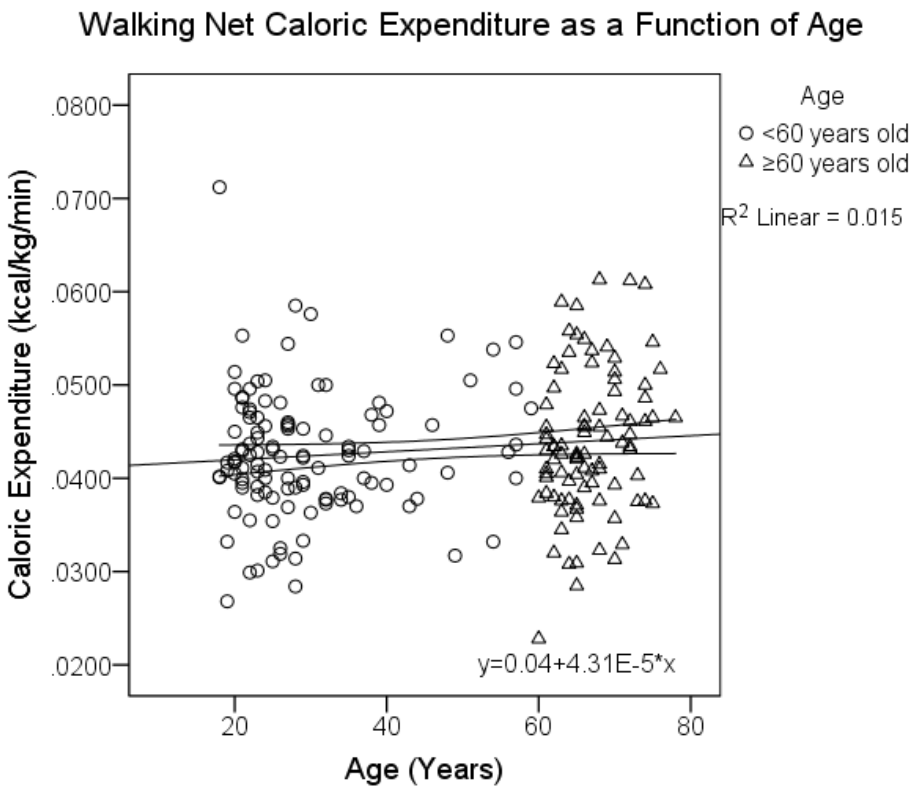

Figure 4. Scatterplot graph showing the relationship between net caloric expenditure and age in adults < 60 years old (circles) and ≥ 60 years old (triangles). Net caloric expenditure = walking caloric expenditure – resting caloric expenditure. Values are caloric means (kcal/kg/min) from the last five minutes of walking at 3 mph (1.34 m)

APPENDIX L

THE RELATIONSHIP BETWEEN GROSS CYCLING OXYGEN UPTAKE AND AGE

APPENDIX L

THE RELATIONSHIP BETWEEN GROSS CYCLING OXYGEN UPTAKE AND AGE

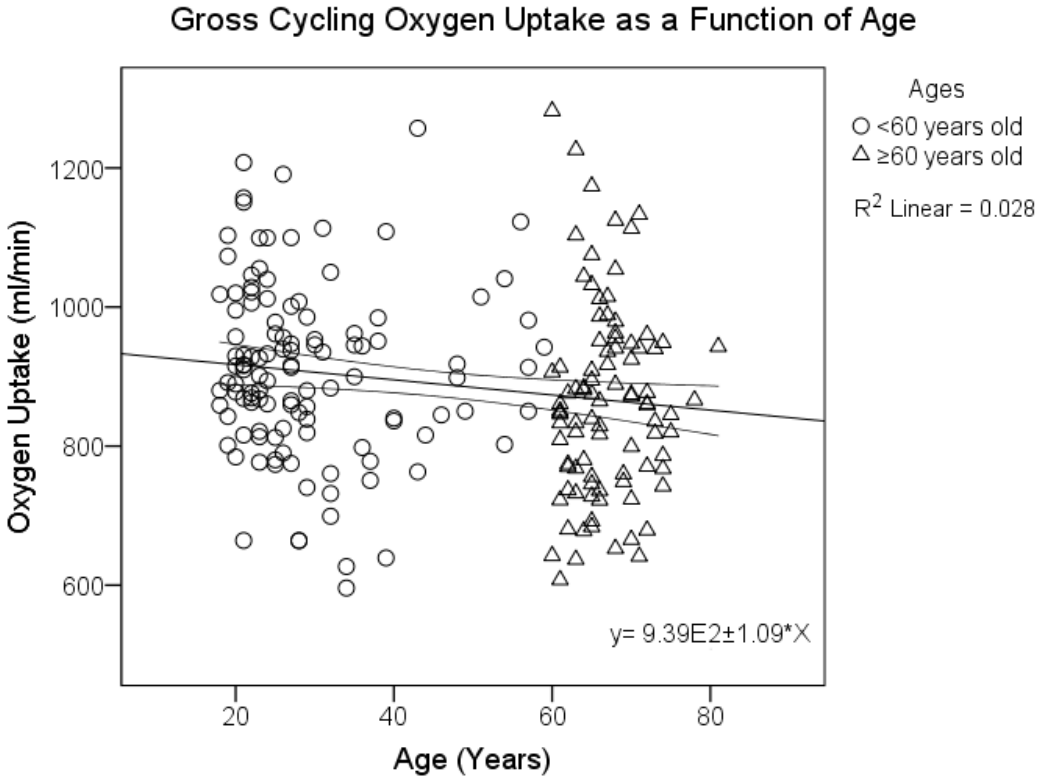

Figure 5. Scatterplot graph showing the relationship between gross oxygen uptake (ml/min) and age in adults < 60 years old (circles) and ≥ 60 years old (triangles). Values are means from the last five minutes of cycling at 50 watts (60-70 rpm).

APPENDIX M

THE RELATIONSHIP BETWEEN NET CYCLING OXYGEN UPTAKE AND AGE

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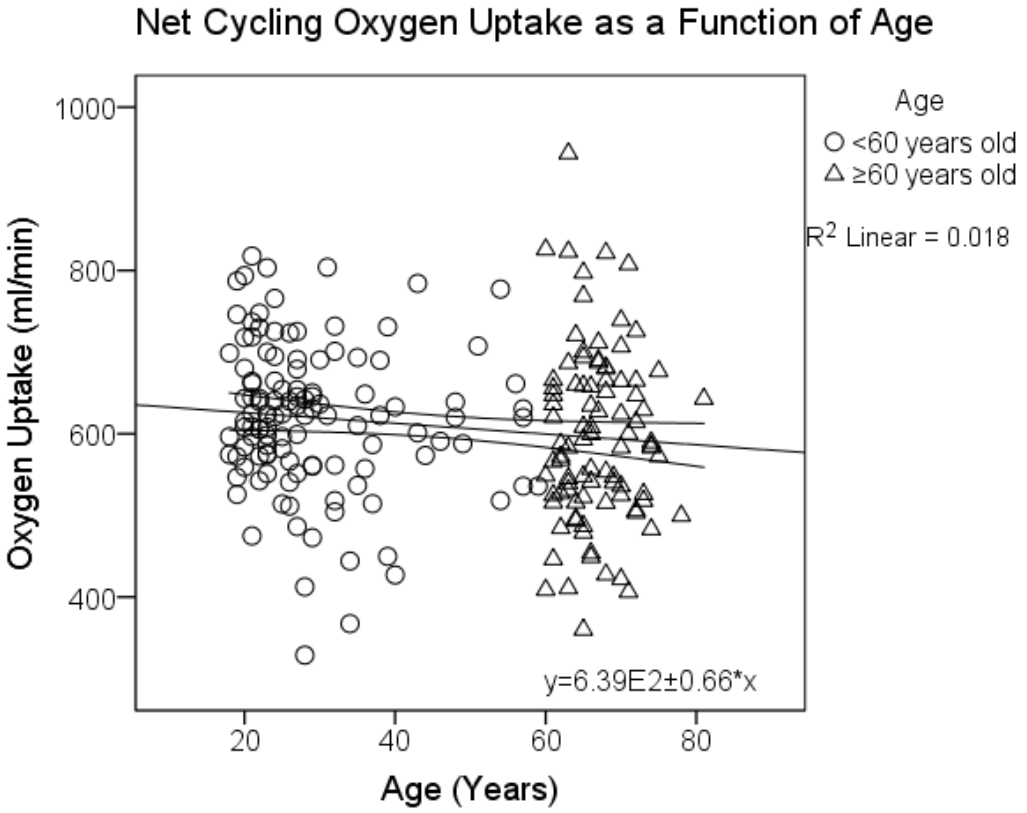

Figure 6. Scatterplot graph showing the relationship between net oxygen uptake (ml/min) in adults < 60 years old (circles) and ≥ 60 years old (triangles). Net oxygen uptake = cycling oxygen uptake – resting oxygen uptake. Values are means from the last five minutes of cycling at 50 watts (60-70 rpm).

APPENDIX N

THE RELATIONSHIP BETWEEN GROSS COST OF CYCLING AND AGE

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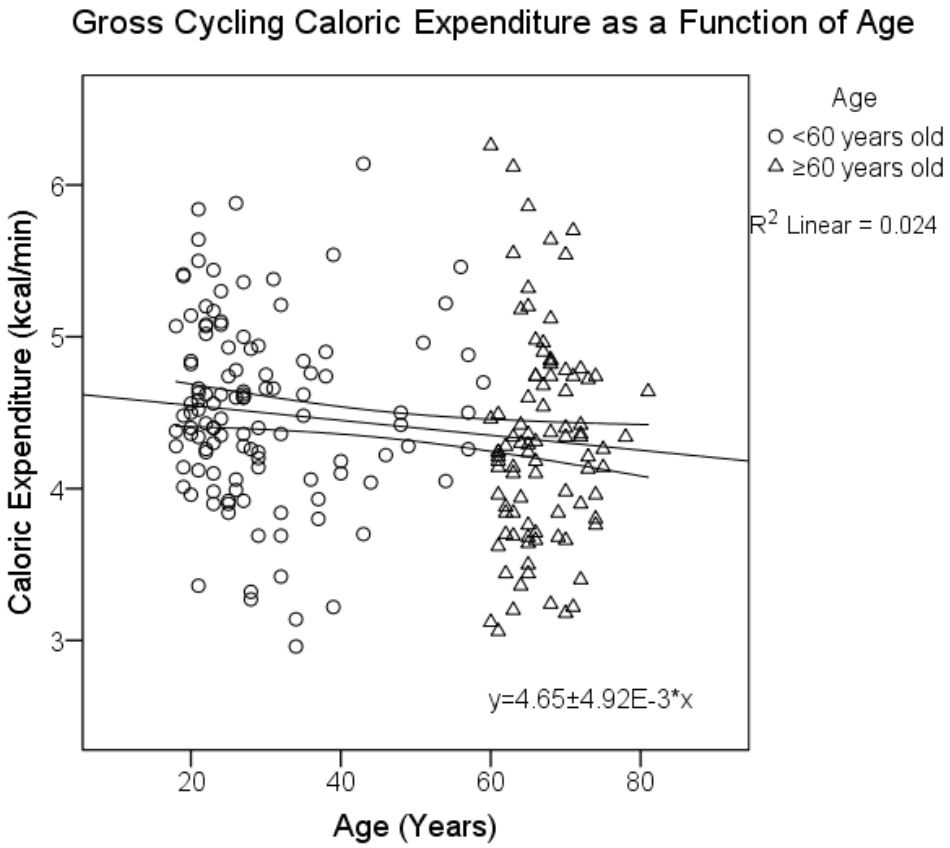

Figure 7. Scatterplot graph showing the relationship between gross caloric expenditure (kals/min) in adults < 60 years old (circles) and ≥ 60 years old (triangles). Values are caloric means from the last five minutes of cycling at 50 watts (60-70 rpm).

APPENDIX O

THE RELATIONSHIP BETWEEN NET COST OF CYCLING AND AGE

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THE RELATIONSHIP BETWEEN NET COST OF CYCLING AND AGE

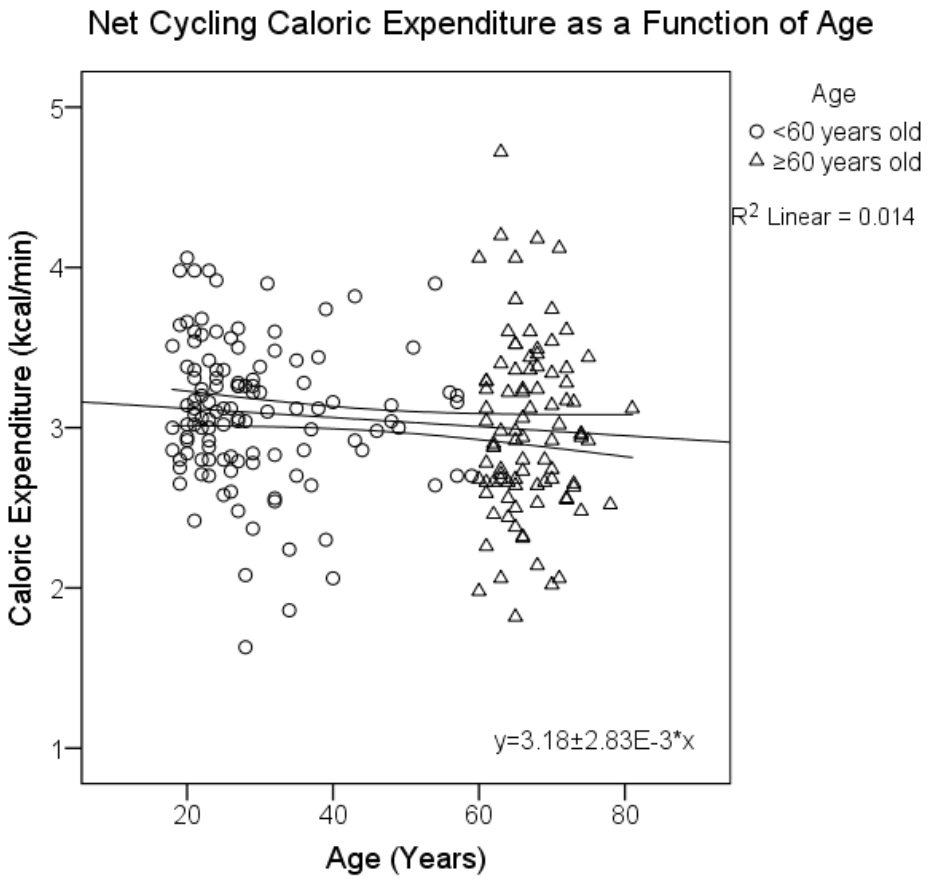

Figure 8. Scatterplot graph showing the relationship between net caloric expenditure and age in adults < 60 years old (circles) and ≥60 years old (triangles). Net caloric expenditure = cycling caloric expenditure – resting caloric expenditure. Values are caloric means (kg/min) from the last five minutes of cycling at 50 watts (60-70 rpm).

APPENDIX P

THE RELATIONSHIP BETWEEN GROSS CYCLING EFFICIENCY AND AGE

APPENDIX P

THE RELATIONSHIP BETWEEN GROSS CYCLING EFFICIENCY AND AGE

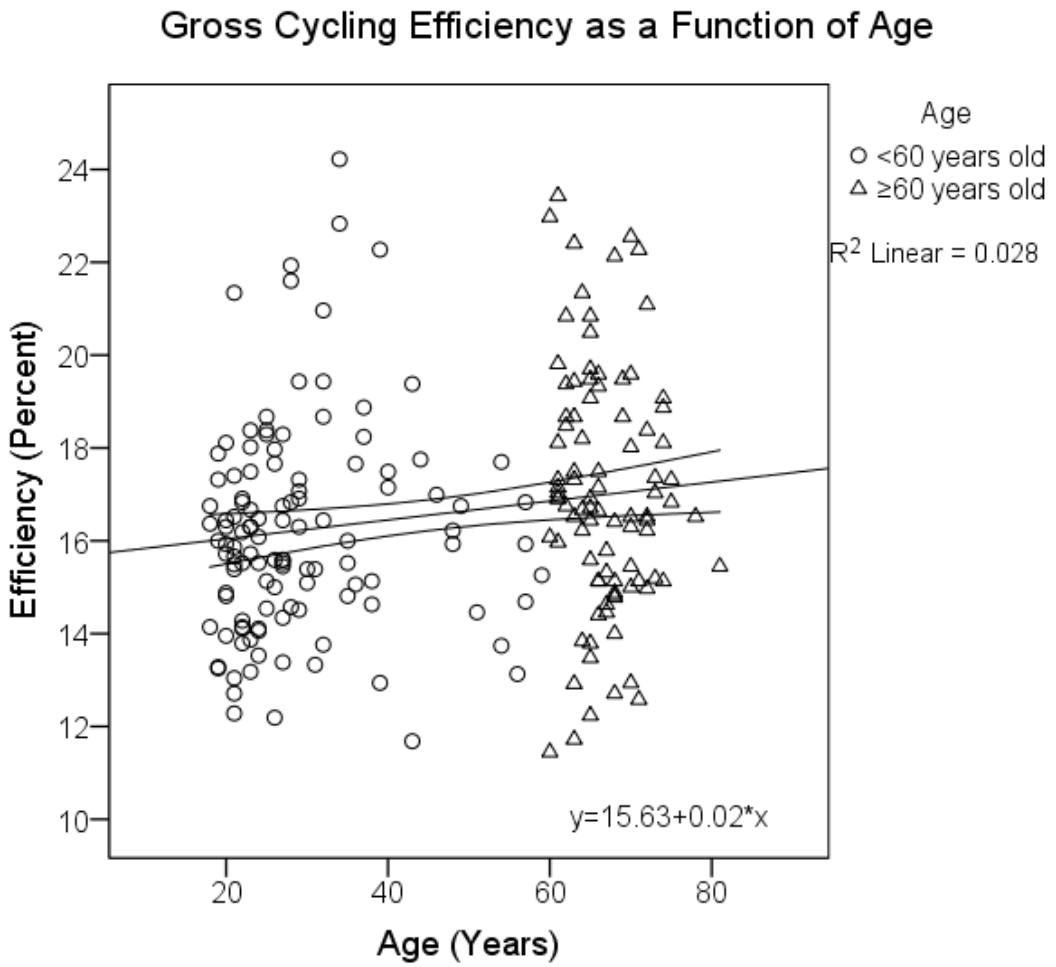

Figure 9. Scatterplot graph showing the relationship between gross cycling efficiency and age in adults < 60 years old (circles) and ≥ 60 years old (triangles). Gross cycling efficiency = caloric equivalent of 50 watts (0.717) / cycling caloric expenditure. Result multiplied by 100 to obtain a percent. Values are derived from caloric means (kg/min) of the last five minutes of cycling at 50 watts (60-70 rpm).

APPENDIX Q

GRAPH OF RELATIONSHIP BETWEEN NET CYCLING EFFICIENCY AND AGE

APPENDIX Q

THE RELATIONSHIP BETWEEN NET CYCLING EFFICIENCY AND AGE

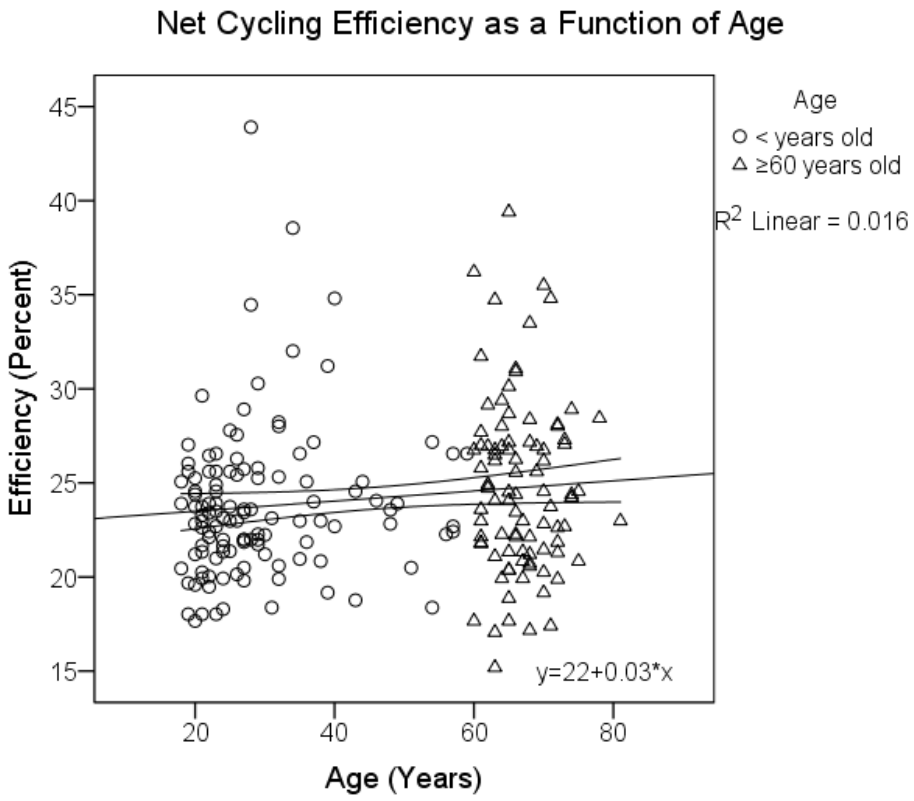

Figure 10. Scatterplot graph showing the relationship between net cycling efficiency and age in adults < 60 years old (circles) and ≥ 60 years old (triangles). Net cycling efficiency = caloric equivalent of 50 watts (0.717) / cycling caloric expenditure – resting caloric expenditure. Result multiplied by 100 to obtain a percent. Values are derived from caloric means (kg/min) from the last five minutes of cycling at 50 watts (60-70 rpm).